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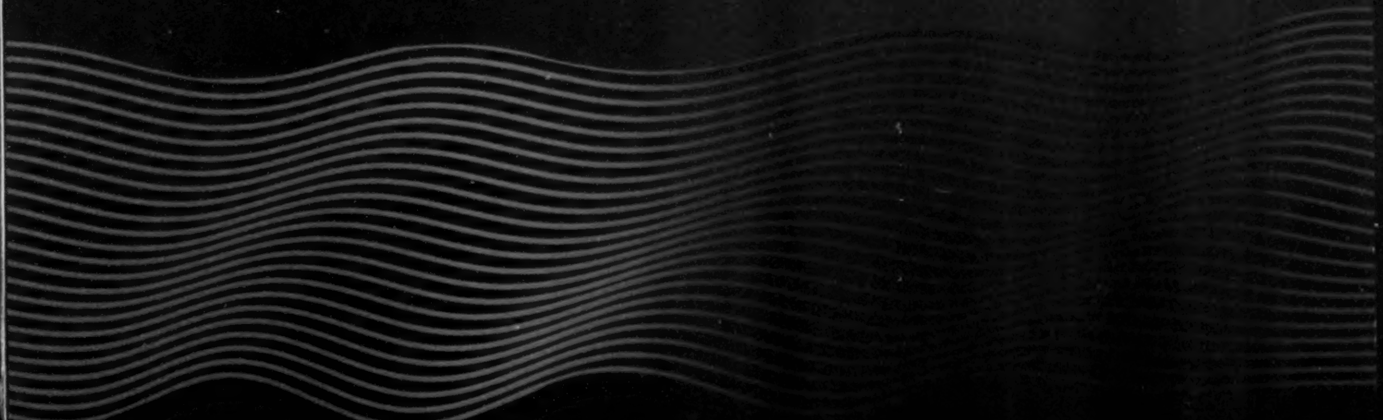

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Distributions of physonect siphonulae in the Gulf of Maine and their potential as important sources of acoustic scattering

Mark C. Benfield, Andone C. Lavery, Peter H. Wiebe, Charles H. Greene, Timothy K. Stanton, and Nancy J. Copley

Abstract: The distributions of siphonulae stages of physonect siphonophores were mapped in Wilkinson, Jordan, and Georges basins of the Gulf of Maine using a video plankton recorder. Siphonulae are often overlooked in net samples and our optical survey appears to be the first in situ investigation of these organisms. Siphonulae were distributed at mid-depths in narrow horizontal layers, suggesting potential control of their buoyancy. The siphonulae possessed gas-filled pneumatophores with diameters of 0.1–0.4 mm. Pneumatophore diameters appeared to be similar over their entire sampled depth range, suggesting that siphonulae may be capable of regulating the pressure of gas within the pneumatophore to maintain a constant volume. The dimensions of the siphonulae pneumatophores placed them near the acoustic resonance region for scattering at 43 kHz when near the surface and 120 kHz when at depth. Theoretical estimates of the acoustical target strengths of gas bubbles of sizes corresponding to the sizes of our measured pneumatophores produced relatively strong backscatter. Layers of siphonulae corresponded to regions of high acoustical backscatter at 120, 200, and 420 kHz.

Résumé : Un système d'enregistrement vidéo du plancton nous a permis de décrire les répartitions des stades siphonulas des siphonophores physonectes dans les bassins Wilkinson, Jordan et Georges du golfe du Maine. Les larves siphonulas sont souvent négligées dans les échantillons au filet et notre inventaire optique semble être la première étude in situ de ces organismes. Les siphonulas se distribuent aux profondeurs moyennes en minces couches horizontales, ce qui fait croire qu'elles ont le pouvoir de contrôler leur flottabilité. Les siphonulas possèdent des pneumatophores de diamètres de 0,1 à 0,4 mm et remplis de gaz. Les diamètres des pneumatophores semblent être semblables dans toute la gamme des profondeurs échantillonnées, ce qui paraît montrer que les siphonulas sont capables de régler la pression gazeuse dans leurs pneumatophores de façon à maintenir le volume constant. Les tailles des pneumatophores des siphonulas avoisinent la région de résonnance acoustique de diffusion à 43 kHz près de la surface et à 120 kHz en profondeur. Les estimations théoriques des forces acoustiques de cibles de bulles gazeuses de tailles correspondant aux tailles mesurées chez les pneumatophores produisent une rétrodiffusion relativement forte. Les couches de siphonulas correspondent à des régions d'importante rétrodiffusion acoustique à 120, 200 et 420 kHz.

[Traduit par la Rédaction]

Introduction

Estimation and prediction of the distributions and abundances of marine organisms are central goals of biological oceanography and constitute specific objectives of programs such as U.S. GLOBEC (Global Ocean Ecosystem Dynamics; U.S. GLOBEC 1992). In the case of marine zooplankton, knowledge of where and when zooplankton taxa occur remains an essential precursor for understanding the population dynamics of both zooplankton and higher trophic levels, particularly fish. The pursuit of these goals has been particularly challenging for oceanographers studying zooplankton because of horizontal and vertical patchiness, avoidance, gear-selectivity, and the fragility of many taxa. Although much has been learned about subadult and adult stages of specific zooplanktors, it is a fair generalization that our cur-

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rent understanding of the ecology of larval and juvenile stages is far more limited.

Physonect siphonophores are a suborder of broadly distributed, colonial, gelatinous organisms of considerable ecological importance because of their capacity for predation on ichthyoplankton and invertebrate zooplankton (Barham 1963). Physonect siphonophores are generally distinguished by the presence of both a gas-filled inclusion called a pneumatophore and a series of one or more medusoid swimming bells called nectophores that are used for propulsion (Totton 1965; Mackie et al. 1987). These colonial organisms are also of potential interest to those undertaking acoustic surveys of the water column because of their disproportionately strong acoustic returns relative to their biomass (Barham 1963; Stanton et al. 1994; Warren et al. 2001). The gas-filled pneumatophore is primarily responsible for the strong acoustic echo from siphonophores, particularly at acoustical frequencies near the resonance frequency of the gas bubble (Stanton et al. 1994, 1998*a*, 1998*b*). Although physonect colonies are known to be strong acoustic scatterers, their contribution to the scattering is easily overlooked during "sea-truthing" surveys because large colonies may be agile swimmers (Barham 1963; Rogers et al. 1978) capable of avoiding many nets or they are severely damaged during the collection process (Totton 1965; Hamner et al. 1975; Warren et al. 2001). When colonies are collected by larger nets such as the multiple opening/closing net and environmental sensing system (MOCNESS), they are often shredded (Greene et al. 1998) and enumeration is based on the presence of recognizable remnants such as pneumatophores and nectophores. Although some net systems such as the Reeve net (Reeve 1981) have been designed to minimize such damage (see Wiebe and Benfield (2001, 2003) for a summary of these and other net systems), our understanding of the ecology of gelatinous plankton has been limited to a large extent by sampling difficulties. The development of in situ observational techniques (e.g., occupied and unoccupied submersibles) and remote image-forming optical survey systems such as the video plankton recorder (VPR; Davis et al. 1992) has substantially advanced our understanding of the ecology of gelatinous plankton.

Physonect siphonophores reproduce by producing sperm and eggs within gonophores. Fertilized eggs are released into the water column where they pass through planulus larval stages and develop into the siphonula stage (Mackie et al. 1987). Although there is some question as to whether siphonulae are true larvae (Sherlock and Robison 2000), we follow their convention and refer to them as a larval stage. Early in the development of the siphonula stage, physonect genera such as *Nanomia* begin to secrete gas into the pneumatophore (Mackie et al. 1987; Sherlock and Robison 2000). With the development of the pneumatophore, the small siphonula stages may be detected acoustically, especially when ensonified at frequencies near the resonance frequency of the gas inclusion. It is well established that adult physonect siphonophores produce strong acoustic echoes near the resonance frequency of the pneumatophore (Barham 1963; Stanton et al. 1994; Warren et al. 2001). Nothing has been reported about the potential for smaller siphonophore stages to scatter sound. Gas-bearing siphonulae are far less likely than adult colonies to be enumerated during net sampling because of their small size and amorphous appearance in preserved samples. If siphonulae produce strong acoustical returns and are difficult to quantify with traditional samplers, it may be difficult to explain the source of strong acoustical scattering in regions where they are abundant.

During analysis of VPR images collected during surveys in the Gulf of Maine, we observed small, unidentified, tentaculate organisms that were subsequently identified as siphonula larvae of physonect siphonophores (Rob Sherlock and Bruce Robison, Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, personal communication). Although the pneumatophores of these siphonulae appeared to be smaller than those of adult colonies by approximately an order of magnitude, our estimates of their acoustical target strengths suggested that these small pneumatophores were still producing relatively strong echoes, especially at the lower portion of our frequency range (43 and 120 kHz) because their gas inclusions were at, or near, resonance. The objectives of this study were (1) to quantify the spatial distributions of physonect siphonulae, (2) to determine the ranges of environmental conditions associated with their distributions, and (3) to estimate their contribution to measured acoustical scattering.

Materials and methods

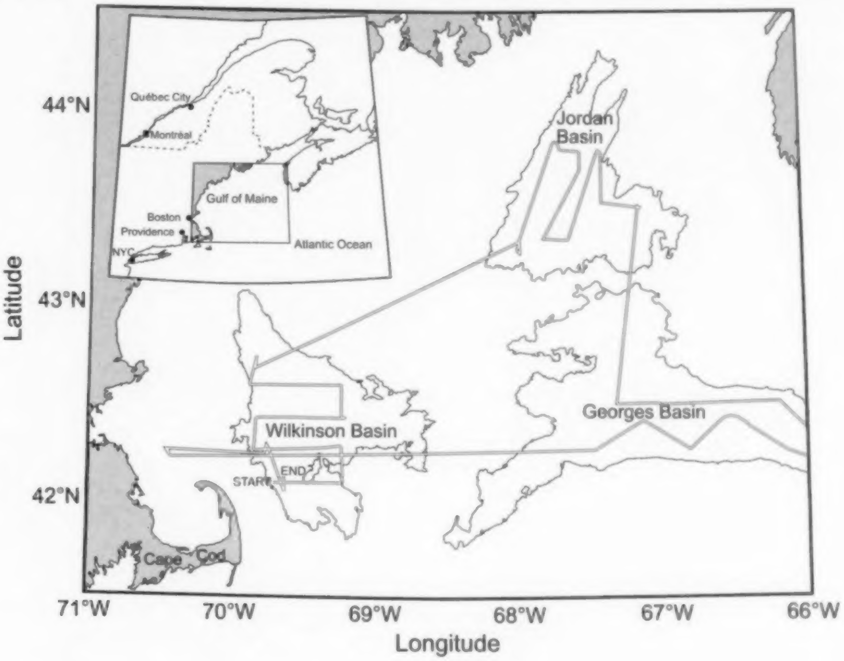
Study area

Our data were collected during a research cruise aboard the R/V *Endeavor* in the Gulf of Maine from 4 to 13 December 1999. This cruise was part of the U.S. GLOBEC program and our primary objective was to quantify the distribution of the diapausing copepod *Calanus finmarchicus* and its primary invertebrate predators — physonect siphonophores such as *Nanomia cara* and the euphausiid *Meganyctiphanes norvegica* — in Wilkinson, Jordan, and Georges basins of the Gulf of Maine (Fig. 1).

Oceanographic surveying

Our surveys were conducted using a high-speed, deep-towed system called BIOMAPER II (bio-optical, multi-frequency acoustical, and physical environmental recorder, a custom-built system constructed by the Woods Hole Oceanographic Institution, Woods Hole, Mass.) that was equipped with five echosounder pairs operating at 43, 120, 200, 420, and 1000 kHz, a single-camera VPR, and a suite of environmental and bio-optical sensors (Wiebe et al. 1997, 2002; Austin et al. 1998). Each pair of transducers on BIOMAPER II was oriented so that one aimed upwards and the other downwards. During surveys, BIOMAPER II was lowered and hauled back in a saw-tooth trajectory, called a towyo, between the surface and within 10–20 m of the bottom to provide maximal coverage of the water column for most sensors, including the highest acoustical frequencies. Vertical descent and ascent rates were typically 5 $m \cdot min^{-1}$ at a horizontal velocity of 6–8 knots. The transducer pairs fired in a cyclical sequence with a ping interval of 2.5 s. Echo integration was performed at the end of each 12-s cycle to provide estimates of volume backscattering, for each frequency, in 1 m thick depth bins to the maximum effective range for each frequency (43 kHz, 200 m; 120 kHz, 200 m; 200 kHz, 150 m; 420 kHz, 100 m; 1000 kHz, 35 m). In this study, we

Fig. 1. The track line of the R/V *Endeavor* in the Gulf of Maine during survey operations conducted from 4 to 13 December 1999. The primary deep basins of the Gulf of Maine (Wilkinson Basin, Jordan Basin, and Georges Basin) are delimited with the 200-m isobaths. The inset map in the upper left corner illustrates the location of the study area within the New England – Maritimes region.



include 43, 120, 200, and 420 kHz data. The limited range of the 1000 kHz transducers made it difficult to interpret echogram patterns and results from 1000 kHz were omitted.

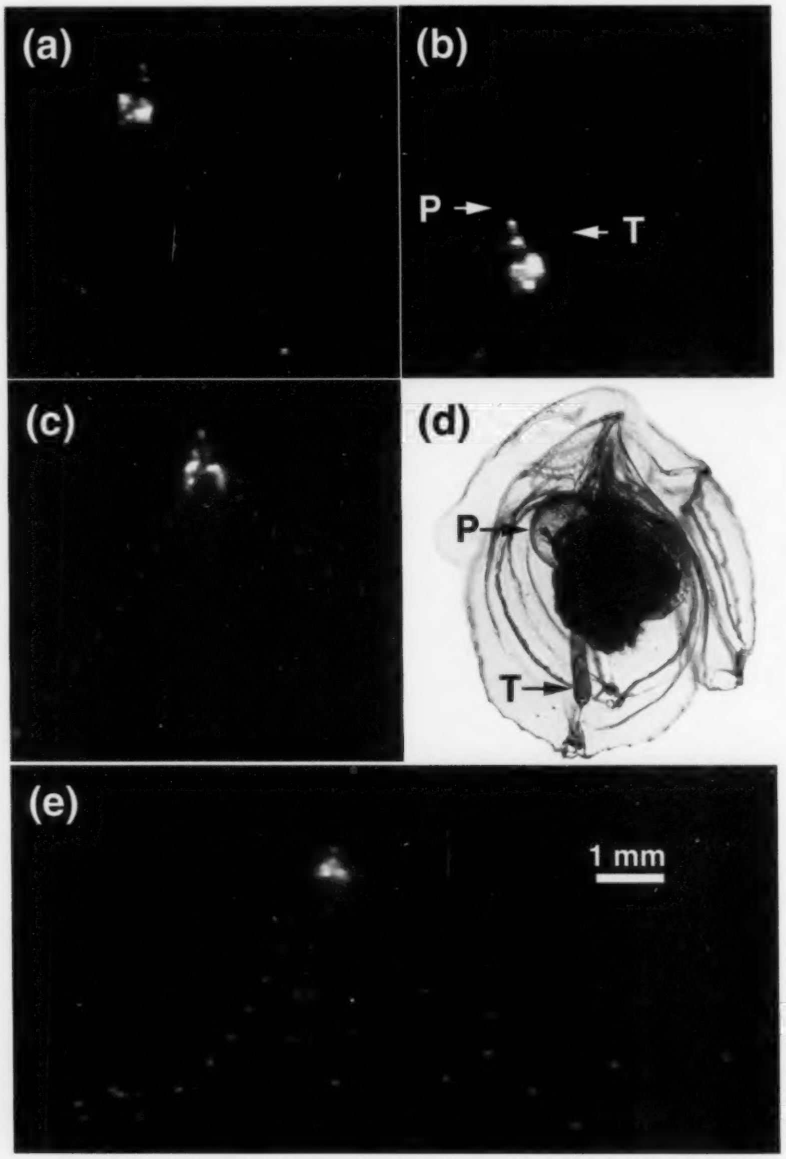
The VPR is an underwater high-magnification video system (Davis et al. 1992) that collects images of plankton within the water column using a high-speed strobe and video camera. Our VPR was a single-camera model that was mounted on the upper front end of BIOMAPER II. It imaged a volume of 5.1 mL at a rate of 60 Hz (18.43 L·min^{-1}). Video data were transmitted to the surface via an electro-optical tow cable, stamped with a time code derived from global positioning system data, and stored on S-VHS format videotape.

Data analysis

Videotapes were postprocessed after the cruise using an image processor (Imaging Technology Inc., Bedford, Mass.) that digitized and then examined each video field for targets that met user-defined criteria for size, brightness, and focus. Targets that met these criteria were termed regions of interest (ROIs) and were written to disk using a filename that represented the elapsed time in milliseconds since midnight (GMT) that each ROI was detected. Because prior testing indicated that one set of ROI extraction parameters was not optimal for all zooplankton taxa, each tape was processed three times with different extraction parameters. Graphical image browsing software (ThumbsPlus 4.10; Cerious Software Inc., Charlotte, N.C.) was then used to eliminate duplicate ROIs and to sort ROIs into taxonomic categories. ROIs containing siphonulae (Fig. 2) were separated from all other targets. Then the time of detection of each siphonula was used to determine the depth, latitude, longitude, and environmental conditions of each individual based on the BIOMAPER II trajectory and environmental sensing system data. The diameters of pneumatophores in ROIs that contained visible pneumatophores (154 individuals out of a total of 175 siphonulae detected by the image processor) were measured using a Matlab program (The Mathworks Inc., Natick, Mass.). The densities of siphonulae were estimated within 10 m thick depth bins along the BIOMAPER II track line by summing the total number of siphonulae detected while BIOMAPER II passed through each 10-m depth stratum and then dividing by the volume of water surveyed in the same interval by the VPR. The volume of water imaged by the VPR within each 10-m stratum varied as a function of the vessel velocity, BIOMAPER II descent rate, and prevailing currents. Based on a 4-h section of tape in Jordan Basin that contained three typical towyos, the mean volume imaged within each 10 m thick depth stratum was 62.0 L. Each density estimate based on the imaged volume was then scaled up to a density within a standard volume (n·m^{-3}).

A 4-h section of tape from the end of our survey of Jordan Basin collected from 1118 to 1522 on 7 December 1999 (341.4713–341.6405 in Julian day format) was also examined manually to determine the extraction efficiency of the image processor for siphonulae ROIs. Each of the two S-VHS tapes were viewed at slow speed using an editing deck, and the S-video output from the deck was routed into a laptop computer (Macintosh Powerbook G3; Apple Computer Inc., Cupertino, Calif.) using a video capture card (Irez Inc.,

Fig. 2. (*a–c*) Examples of larval physonect siphonophores from video plankton recorder (VPR) images collected by BIOMAPER II in the Gulf of Maine during December 1999. (*d*) A preserved siphonula collected with a 1-m^2 MOCNESS net from Jordan Basin at night during the same cruise as the VPR images. The pneumatophore (P) and tentacle (T) are indicated. (*e*) A VPR image that shows a single siphonula with tentacles extended in a fishing posture containing scaling information.



Scottsdale, Ariz.) and video digitizing software (Irez ReelEyes; Irez Inc.). A still image of each manually detected siphonula was stored as a TIFF- or JPEG-formatted image using the time code as a file name. The file names of all manually located siphonulae were read into Matlab and converted to local time (Julian day with January 1 = day 1). The positions of these siphonulae were then superimposed over the acoustics record from BIOMAPER II to evaluate whether the abundances of siphonulae were associated with patterns of elevated acoustical scattering. Finally, the number of siphonulae detected manually was compared with the number detected semiautomatically to determine the extraction efficiency of the image processor.

The vertical distributions of siphonulae were estimated in 10-m depth bins beginning at the surface and extending to the maximum depth surveyed. Vertical distributions were estimated during the day and night for each basin in the Gulf of Maine. Wilkinson Basin was visited twice during the cruise, and both surveys in that area were examined separately because several days separated the two surveys. Day distributions included all siphonulae detected from 1 h after the average time of sunrise (0650 local time) until 1 h before the average time of sunset (1600 local time). Night distributions included all siphonulae detected from 1 h after sunset until 1 h before sunrise.

Periodic net samples were collected with a 1-m^2 MOCNESS sampler equipped with 335 μm mesh nets. Samples from one net cast collected in Jordan Basin between 2255 and 2308 on 6 December 1999 (Julian day 340.9549–340.9639) were examined for siphonulae. Although the MOCNESS is not likely to provide a quantitative record of siphonulae distributions, it does retain some fraction of the siphonulae that enter the nets. We measured the diameters of all preserved siphonula pneumatophores that were recovered from each of the eight nets with an optical micrometer and a microscope to compare the size distributions of net-sampled siphonulae with those measured from VPR images.

The exact modal series solution to the wave equation for scattering from a fluid sphere (Anderson 1950) was used to predict the scattering from each measured siphonula pneumatophore (from VPR images). Details of this methodology and associated assumptions are provided in Appendix A.

We estimated the contribution to volume scattering at 43, 120, 200, and 420 kHz by siphonulae for the 4-h section of the acoustic record from Jordan Basin that corresponded to the visually examined section of videotape. The acoustic data were separated into three towyo sections. Within each towyo section, the mean volume backscattering coefficient ($\bar{s}_v$) was estimated by averaging all measured s_v values within each 10 m thick stratum from 0 to 200 m. The forward problem (prediction of acoustic scattering from VPR-derived numbers and sizes of individuals) was then solved in the following manner. For each 10-m stratum, the predicted backscattering cross section of every pneumatophore was estimated for each of the four acoustical frequencies by accounting for the density of siphonulae in the corresponding size class per cubic metre within the stratum (Appendix A). This yielded an estimate of the contribution to the measured volume backscattering coefficient (s_v) by siphonulae in each depth stratum. The percent contribution of siphonulae to measured volume backscattering coefficients in each depth stratum within each of the three towyos was then estimated as $\frac{s_{v_{\text{siphonulae}}}}{\bar{s}_v} \times 100$.

Results

Spatial distributions

Of 175 siphonulae detected by the image processing system from survey operations in the Gulf of Maine, all but three were found in the waters over one of the three surveyed basins, and the remainder were imaged during transit from one basin to the next. The distributions of siphonulae were highly patchy. Some dense patches were encountered in surface waters of Wilkinson Basin; however, most siphonulae were distributed at mid-depths in all three basins (Fig. 3) and often formed well-defined horizontal layers. Siphonulae tended to be distributed deepest in Georges Basin and shallowest in Wilkinson Basin (Figs. 3, 4).

Siphonulae were small and rather faint images on the videotape. Consequently, our image processor had a relatively low extraction efficiency of 36.7% based on comparisons between ROIs detected by the image processor and our manual examination of 4 h of tape. Thus, the 175 animals detected by the processor likely represented the presence of over 450 individuals. Estimates of the densities of siphonulae in the water column based on the manually detected data set indicated that siphonulae could be present in relatively high numbers (up to 96.6 siphonulae·m^{-3}), although the mean density of 8.2 siphonulae·m^{-3} was considerably lower.

The existence of a diel vertical migration pattern was not clearly supported in all three basins (Fig. 4). Wilkinson Basin was the only region in which differences in the day and night distributions suggested a pattern of vertical migration. During the day, siphonulae were detected in the depth range of 40.7 to 188.5 m (median of 75.4 m, mean of 78.5 m). At night during the primary survey, siphonulae were observed in the depth range of 5.1 to 127.4 m (median of 65.9 m, mean of 54.8 m) in a strongly bimodal distribution with one mode in the depth range 70 to 80 m and a second in the upper 10 m (Fig. 4). During subsequent operations in Wilkinson Basin that were conducted after dark, the vertical distribution was strongly skewed towards the surface with most siphonulae in the upper 10–20 m of the water column (Fig. 4). In Jordan Basin, siphonulae displayed similar day and night distributions (Fig. 4), although there was some indication that animals were present at shallower depths and that the center of the distribution rose during the night. During the day, they were detected in the depth range of 24.4 to 173.3 m in a unimodal distribution (median of 104.7 m, mean of 106.4 m; Fig. 4). At night, siphonulae were detected from 5.1 to 149.5 m in a unimodal distribution (median of 98.1 m, mean of 98.0 m). Only two siphonulae were detected during the day over Georges Basin, and both were present below 100 m (Fig. 4). At night, siphonulae were present in the depth range of 9.5 to 149.5 m. Although a few animals were present at the surface, most were concentrated at depth (median of 116.1 m, mean of 107.7 m).

Physical conditions associated with siphonulae

Siphonulae were most abundant in waters warmer than 8.25°C in all three basins (Fig. 5). The mean temperatures of waters where siphonulae were detected were 8.85, 9.82, and 9.89°C for Wilkinson, Jordan, and Georges basins, respectively. Salinity appeared to have less influence on the distributions of siphonulae than did temperature. Wilkinson Basin was fresher than the other two basins and siphonulae in Wilkinson were most abundant in the range of 32.5 to 33.5‰ (mean of 33.03‰; Fig. 5). In the more saline Jordan and Georges basins, most siphonulae were found in the range of 33.75 to 34.75‰ waters (Jordan mean of 34.09‰, Georges mean of 34.24‰; Fig. 5). In Georges Basin, most siphonulae were located within the 26.2–28.0 σ-theta density contours, whereas in Wilkinson and Jordan basins, most siphonulae were located within a narrower range of less dense water that occupied a broader extent of the water column (Fig. 3; Wilkinson range of 25.4 to 26.0 σ-theta and Jordan range of 26.0 to 26.6 σ-theta). There was no consistent relationship between fluorescence and the distributions of siphonulae in any of the basins. In general, siphonulae were more common

Fig. 3. Distributions of physonect siphonulae detected with the video plankton recorder in Wilkinson Basin during (*a*) the primary survey and (*b*) the secondary survey, (*c*) Jordan Basin, and (*d*) Georges Basin. The shaded regions delimit the range of density isopycnals (σ-theta) that contained the majority of siphonulae in each basin. There was insufficient coverage of the water column during the secondary survey of Wilkinson basin to contour the isopycnals.

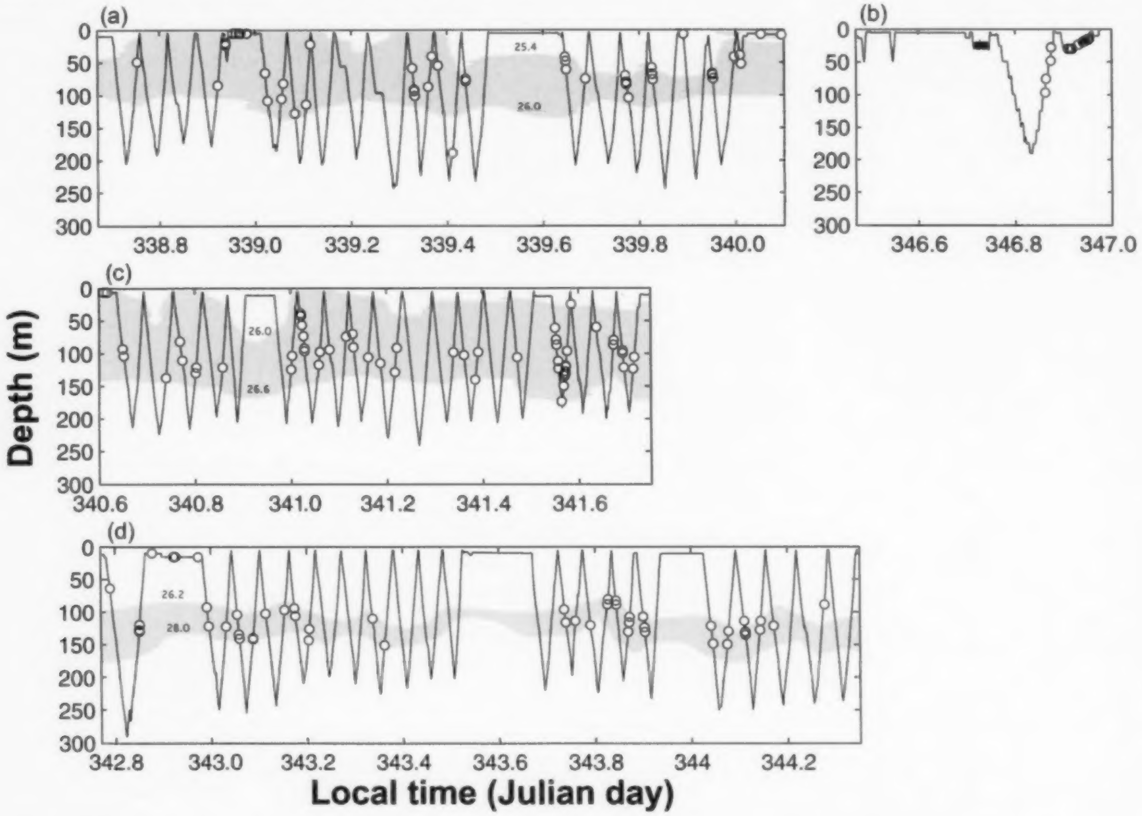
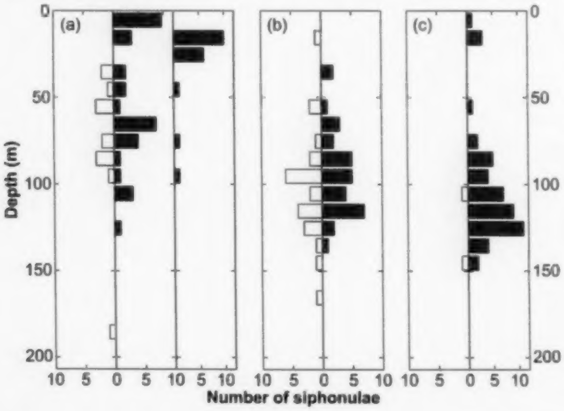


Fig. 4. Vertical distributions of siphonulae during day (sunrise + 1 h to sunset – 1 h; open bars) and night (sunset + 1 h to sunrise – 1 h; solid bars) in (*a*) Wilkinson Basin, (*b*) Jordan Basin, and (*c*) Georges Basin. There are two nighttime distributions for Wilkinson Basin because it was surveyed at the beginning of the cruise and limited survey operations were conducted again during nighttime at the end of the cruise.

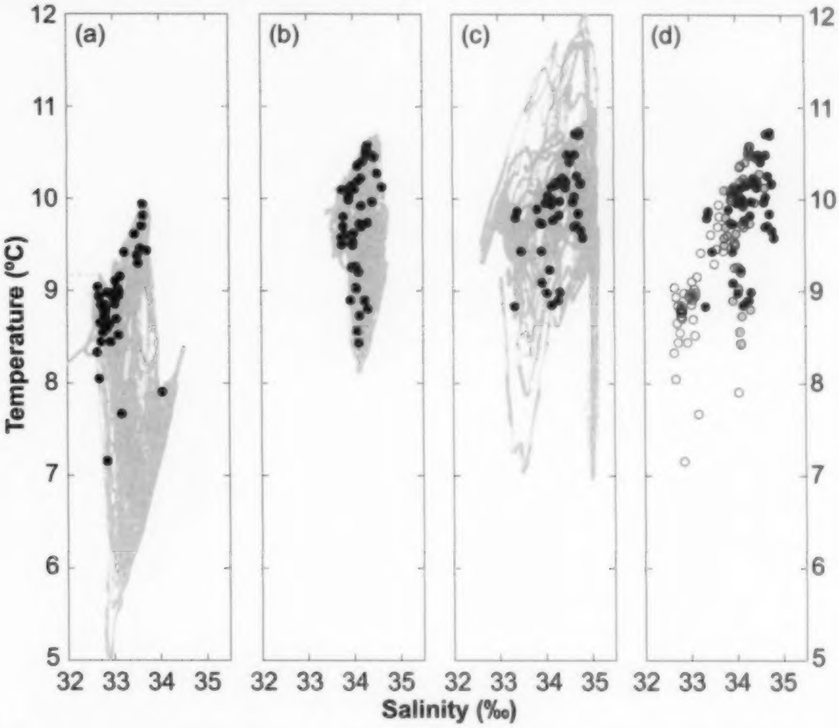


at the lower end of the range of fluorescence values that occurred in the surveyed zone of each basin.

Comparisons of predicted and measured acoustic scattering by siphonulae

The size distribution of 154 measured siphonulae pneumatophores was approximately normally distributed with a mean diameter of 0.21 mm and a median of 0.20 mm (Fig. 6*a*). A regression of pneumatophore diameter on depth was nonsignificant (R^2 = 0.003, p = 0.46), and the pneumatophore diameters did not appear to change substantially with depth (Fig. 6*b*). The mean diameter of pneumatophores from 229 siphonulae collected from Jordan Basin with a 1-m^2 MOCNESS during the late evening (2255–2308 local time) of day 340 was 0.21 mm (range of 0.1 to 0.4 mm). The pneumatophores from the MOCNESS nets had a size distribution that was similar to that of the VPR with some elevated frequencies of smaller diameters that was consistent with postcollection loss of gas. The predicted acoustical target strength (TS) of siphonulae pneumatophores was sensitive to changes in the diameter of the gas bubble (Fig. 6*c*) and hydrostatic pressure (Fig. 6*d*). As the pneumatophore diameter decreased, the resonance frequency increased. At 100-m depth, larger pneumatophores with

Fig. 5. Temperature–salinity (*T–S*) data (shaded areas) from BIOMAPER II surveys in (*a*) Wilkinson, (*b*) Jordan, and (*c*) Georges basins overlaid with the *T–S* conditions measured at points where siphonulae were detected (●). (*d*) The combined *T–S* conditions from all observations of siphonulae in the three basins: Wilkinson (○), Jordan (shaded circles), and Georges (●).

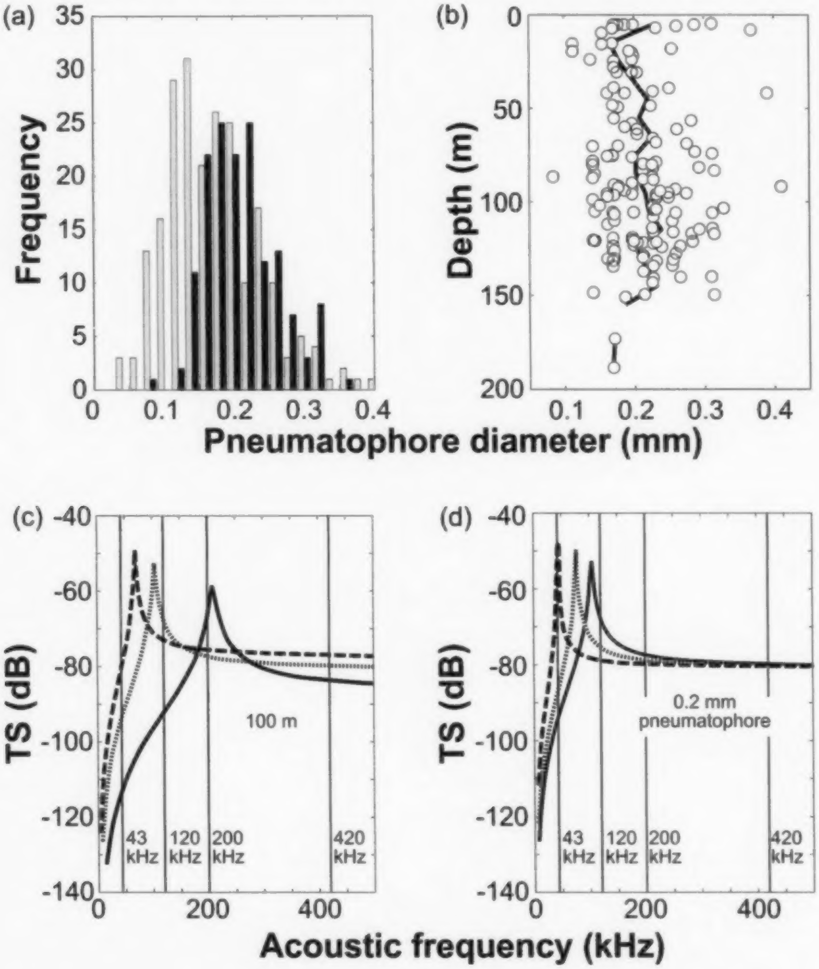


diameters of ~0.3 mm were near resonance at 43 kHz, whereas pneumatophores near the mean diameter (0.21 mm) were close to resonance at 120 kHz, and small pneumatophores (0.1 mm) were within the resonance region at 200 kHz (Fig. 6*c*). For a 0.2 mm diameter pneumatophore, the resonance frequency increased while the scattering amplitude decreased with increasing depth as the hydrostatic pressure compressed the gas within the pneumatophore (Fig. 6*d*). Peak resonance occurred at ~10-m depth at 43 kHz and at ~100-m depth at 120 kHz (Fig. 6*d*). The distributions of TS values estimated from the scattering model for the measured pneumatophores detected by the image processor were narrow at the higher frequencies (200 and 420 kHz) and broader at the lower frequencies (43 and 120 kHz) where resonance was occurring. The mean and median TS values were lowest at 43 kHz (mean of –89.1 dB, median of –90.2 dB), highest at 120 kHz (mean of –72.0 dB, median of –72.4 dB), and both intermediate and similar at 200 kHz (mean of –77.2 dB, median of –76.9 dB) and 420 kHz (mean of –79.6 dB, median of –79.8 dB).

An examination of the acoustic record from BIOMAPER II coincident with the 4 h of manually examined videotape suggests that the presence of siphonulae at depth was associated with enhanced scattering at 120 kHz (Figs. 7, 8). In general, the presence of siphonulae in the video corresponded with regions of strong scattering, although the strongest scattering was not always coincident with the highest siphonulae densities. A zone of elevated scattering of approximately –60 dB was generally present at 120 and 200 kHz within the depth interval 50–150 m (Fig. 7). At the higher and lower frequencies, we observed consistent bands of elevated scattering that corresponded to the depth interval at which siphonulae were detected (Fig. 7), although at generally lower scattering levels. In addition, although elevated scattering at 43 kHz is indicated in the vicinity of the vehicle coincident with siphonulae, this scattering did not extend away from the vehicle and this is potentially an artifact that is currently under investigation. The estimated contributions by siphonulae to measured scattering at each of the four frequencies suggest that they can account for much of the observed scattering in regions where they are abundant (Fig. 8). Further, the shapes of the vertical distribution of predicted scattering from siphonulae and measured scattering from BIOMAPER II were generally similar at all frequencies (Fig. 8).

The MOCNESS tow taken in Jordan Basin revealed a mesozooplankton community that was numerically dominated by large and small copepods and ostracods (Fig. 9). Other taxa that are potentially strong scatterers such as thecosomate pteropods, euphausiids, and adult siphonophores were generally present in low densities. Small copepods dominated the zooplankton assemblage at the surface, whereas larger copepods (primarily *Calanus finmarchicus* and *Paraeuchaeta norvegica*) were abundant at depth (Fig. 9). When the sizes and densities of all taxa except siphonulae collected by the MOCNESS nets were used to predict the acoustic scattering profile (Fig. 9), the difference between the mean measured and predicted scattering strengths demonstrated a substantial

Fig. 6. (*a*) Size–frequency distributions of pneumatophore diameters from siphonulae larvae imaged by the video plankton recorder (solid bars) and recovered from the MOCNESS (shaded bars). (*b*) Scatterplot of pneumatophore diameter and depth for 154 siphonulae. The solid line indicates the mean diameter at 10-m intervals. (*c*) Theoretical scattering curves for 0.1 mm (solid line), 0.2 mm (dotted line), and 0.3 mm (dashed line) diameter siphonula pneumatophores at 100-m depth. (*d*) Theoretical scattering curves for a 0.2 mm diameter pneumatophore at 10-m (dashed line), 50-m (dotted line), and 100-m (solid line) depths.



underestimation of the mean measured scattering in the depth strata in which siphonulae occur. The discrepancy between the mean measured and predicted scattering strengths could have been due to the presence of siphonulae.

Discussion

Siphonulae of *Nanomia bijuga* are able to secrete gas into their pneumatophore after 3–5 days of age (Sherlock and Robison 2000). The presence of a buoyant organ provides the siphonulae with potential control over their vertical distributions. Whether or not siphonulae are capable of depth regulation has not been determined (Sherlock and Robison 2000) and little is known about the vertical distributions of larvae. Bigelow (1911) reported that the larvae of three different genera including *Nanomia* (which had been classified as *Physophora*) were taken at depths from 100–900 m during summer in the Mediterranean Sea. If the distributions that we observed in all three basins were a consequence of active depth regulation, then they suggest that siphonulae are capable of fairly precise control over their depths. Passive accumulation of siphonulae in density strata where they are neutrally buoyant is also possible; however, the range of densities within which siphonulae were most common varied among the three basins. It seems more likely that the siphonulae were distributed within favorable temperature strata and were able to modify their depth distributions to some extent.

Control over their vertical distribution provides siphonulae with the ability to regulate their thermal regime. Bigelow (1911) reported that temperature was the primary determinant of the vertical distributions of siphonophores. This may

Fig. 7. A 4-h section of the acoustic record at (*a*) 43 kHz, (*b*) 120 kHz, (*c*) 200 kHz, and (*d*) 420 kHz from BIOMAPER II near the end of the survey of Jordan Basin on 7 December 1999 (Julian day 341). The presence of individual siphonulae determined from visual examination of videotapes is indicated by the open circles along the trajectory of BIOMAPER II. The three towyos that are indicated correspond to the zones used for subsequent forward problem calculations.

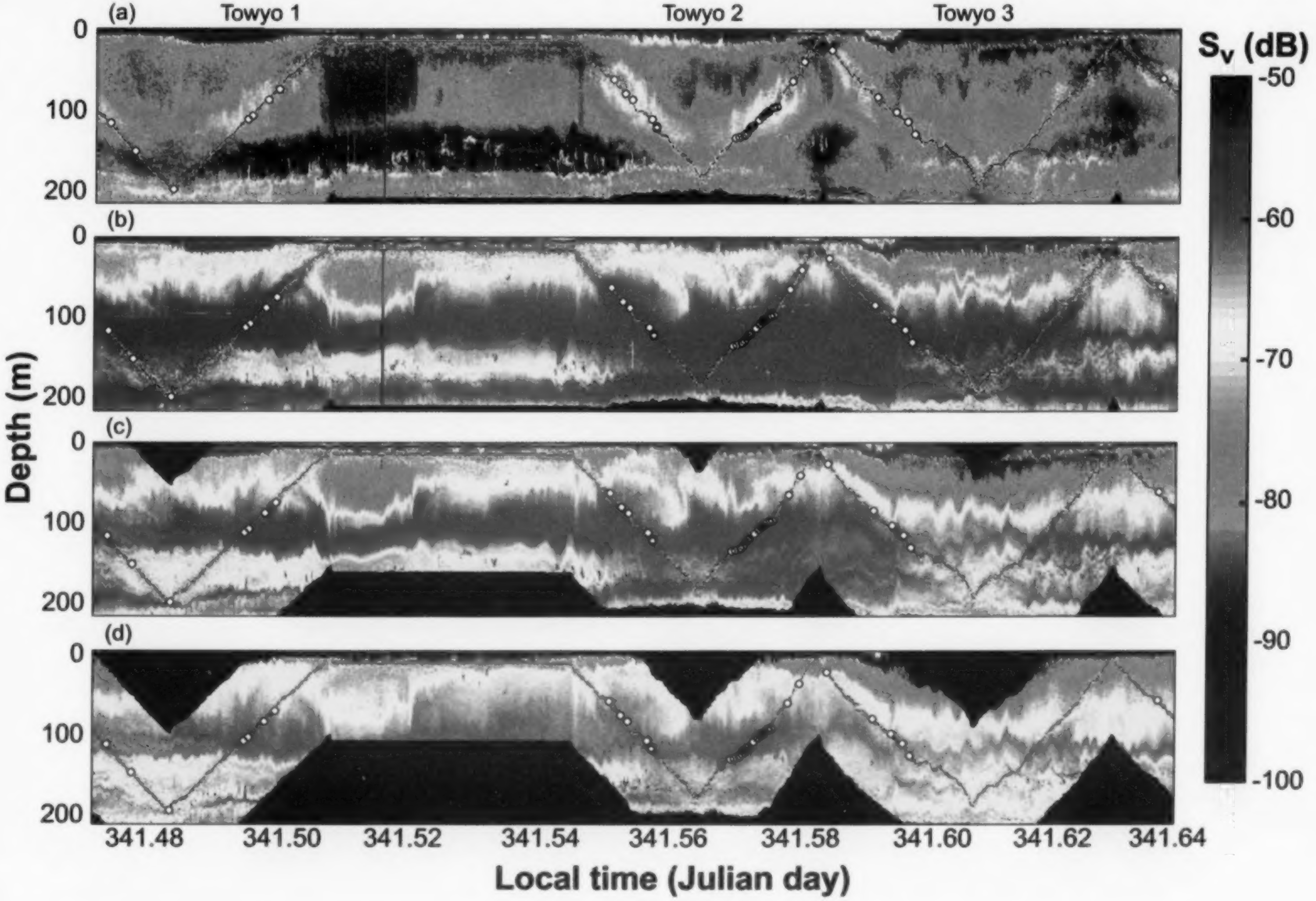
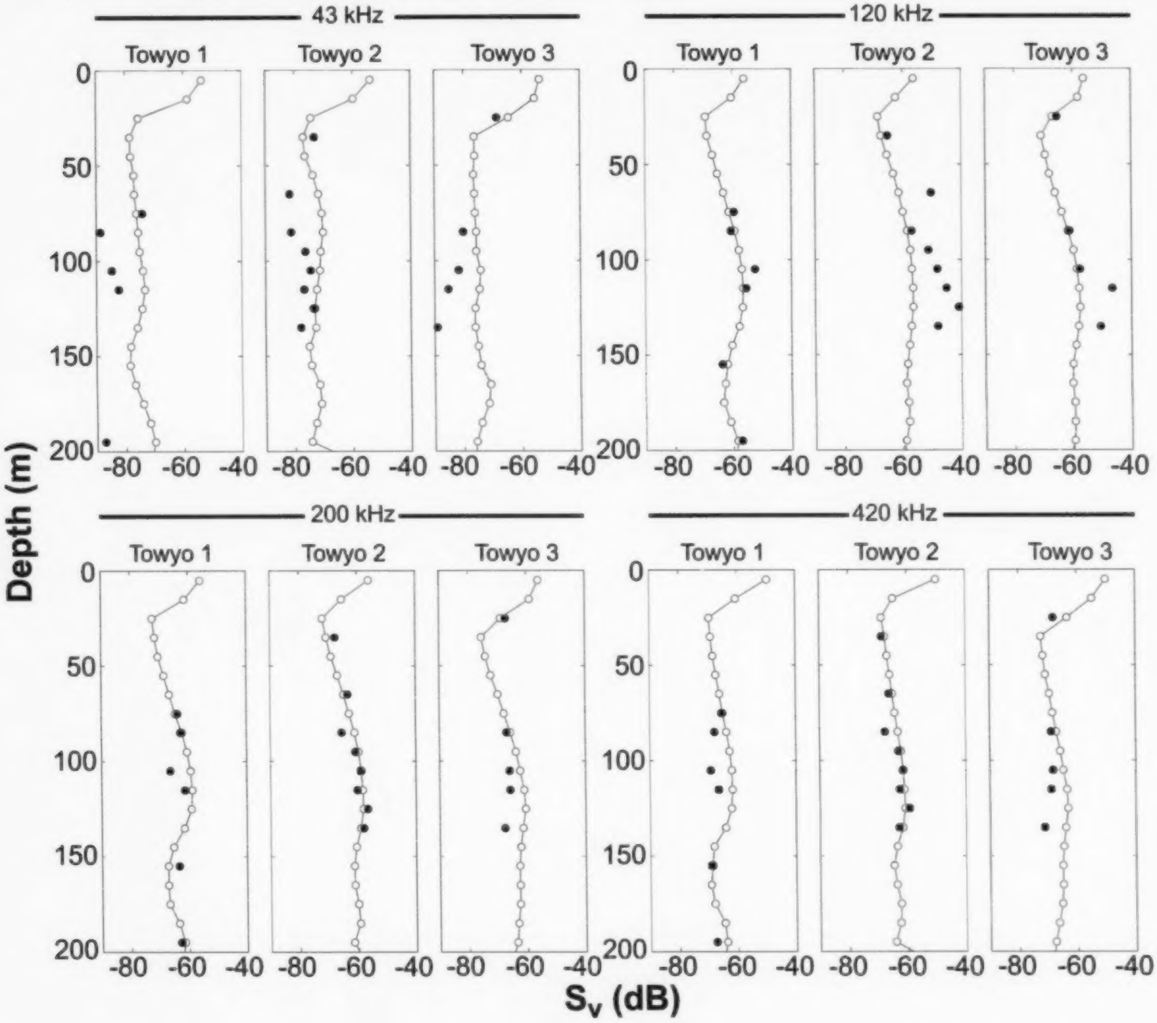


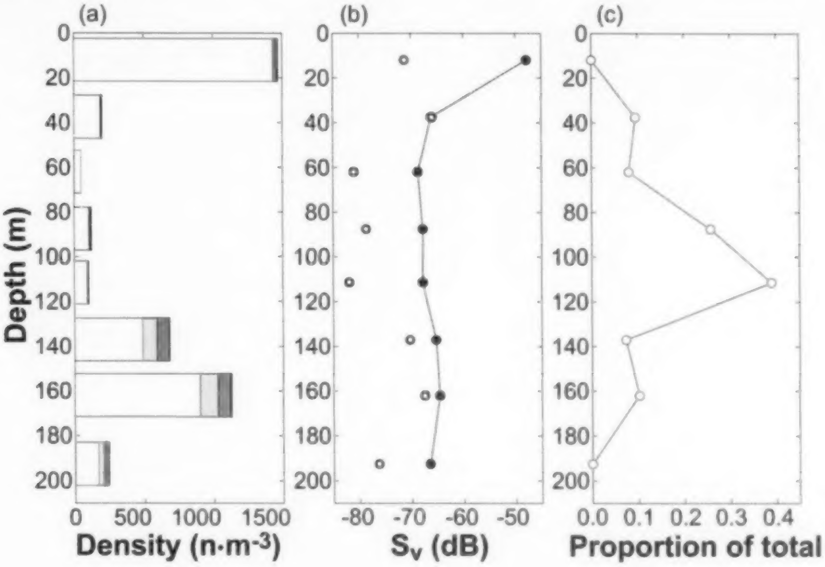
Fig. 8. Mean measured volume backscattering strengths (S_v) at 43, 120, 200, and 420 kHz, within 10-m depth intervals (○) in each of the three towyos demarcated in Fig. 7. The estimated volume scattering strengths (●) attributable to siphonulae are the product of siphonulae densities determined by the VPR in each depth stratum and the predicted backscattering cross section(s) of each of the pneumatophore(s) detected in each towyo stratum at each of the four frequencies.



be important in optimizing conditions for growth and survival. Sherlock and Robison (2000) have demonstrated that the survival and growth of *N. bijuga* siphonulae was temperature dependent. It is interesting that the siphonulae that we observed tended to favor waters between 8 and 11°C. Survival of Sherlock and Robison's siphonulae was higher at 8°C than at 12 or 18°C, although their larvae were not fed and the lower temperature may have favored survival by reducing metabolic rates and slowing the rate of starvation. Although the diets of siphonulae are not well known, it is likely that they include microzooplankton prey items too small to be reliably detected or censused by our VPR and small mesozooplanktors. Fluorescence was one potential indicator of areas of elevated chlorophyll and potentially elevated microzooplankton; however, siphonulae were not associated with regions of elevated fluorescence. Our surveys were conducted in December when primary production was already low and fluorescence may not have been well correlated with microzooplankton abundance. Although Sherlock and Robison (2000) demonstrated that fertilized eggs of *N. bijuga* were capable of developing into siphonulae in the absence of food, most siphonulae that we detected appeared to have a pair of extended tentacles suggesting that they were actively feeding on unknown prey. Based on the abundance of mesozooplankton and presumed abundance of microzooplankton in the Gulf of Maine during our survey, it is likely that the waters in which our siphonulae were distributed contained sufficiently abundant prey siphonulae.

The results from Wilkinson Basin suggest that siphonulae may exhibit a diel vertical migration pattern. Adult colonies

Fig. 9. (*a*) Numerical taxonomic composition of the MOCNESS tow in Jordan Basin conducted in the late evening of 6 December 1999. Each bar is placed at the center of the depth interval for the corresponding net. Small copepods (≤2.5-mm prosome length) are represented by open bars and large copepods (>2.5-mm prosome length) are represented by lightly shaded bars. Ostracods are represented by darkly shaded bars, and other taxa are represented by solid bars. (*b*) The mean volume scattering strength for depth intervals that corresponded to the MOCNESS nets (●). We used the densities and sizes of each taxon in each of the MOCNESS nets to estimate the volume scattering that would be produced from such an assemblage. The predicted scattering for all taxa except siphonulae is indicated by the single points (○). (*c*) The vertical distribution of siphonulae collected by the MOCNESS expressed as a fraction of the total number collected.



of *N. bijuga* have been reported to undertake diel vertical migrations off Italy (Barham 1963), and there was some indication that the distribution of the same species was shifted upward at night in Monterey Bay (Robison et al. 1998). The apparent diel vertical migration pattern that we observed in Wilkinson Basin was not evident in the other two basins. This may simply reflect behavioral plasticity of the siphonulae or an insufficiently large enough sample size to gain a complete picture of their vertical distributions. It is also possible that our inability to determine the species of siphonophores from VPR images has resulted in the pooling of larvae from two or more species that each exhibited different vertical distribution patterns. The taxonomic identities of our siphonulae are unknown because the VPR images do not provide sufficient detail to determine the genus or species. Identification of species from images alone is difficult, and Totton (1965) pointed out that siphonulae of different species of siphonophores appear very similar. We suspect that the siphonulae that we imaged may belong to the genus *Nanomia* because adult *N. cara* were present in the waters of the Gulf of Maine during our cruise. Rogers et al. (1978) reported that adult colonies of *N. cara* were abundant in the waters over the deep basins of the Gulf of Maine during the winter.

Siphonophores are believed to be able to maintain the diameter of their pneumatophore by secreting or absorbing carbon monoxide gas (Mackie et al. 1987). This also appears to be the case for siphonulae because the pneumatophore diameters did not appear to change with depth — a proxy variable for hydrostatic pressure. If we assume a spherical pneumatophore geometry, then a 0.21 mm diameter pneumatophore at 10-m depth (2 atm) would contain 0.0084 μL of gas. To maintain the same pneumatophore volume at 100 m (11 atm), a siphonula would need to secrete an additional 0.004 μL of CO to restore the pneumatophore volume in 1 h after a downward migration of 100 m. Larimer and Ashby (1962) provided estimates of CO gas secretion rates for siphonophores of the species *Physalia physalis* ranging in pneumatophore volume from 25 to 120 mL. We are not aware of any estimates of the gas production rates of physonect genera such as *Nanomia*; however, a sigmoid curve predicting gas production as a function of pneumatophore volume provided a good fit to Larimer and Ashby's data for *P. physalis* (adjusted $R^2 = 0.993$, $p = 0.003$; our fit excluded one apparent outlier for a 14 mL pneumatophore). The gas production rate for a 0.21 mm diameter pneumatophore predicted using the fitted curve was 0.003 μL CO·h^{-1}, which agreed closely with our estimate of 0.004 μL CO·h^{-1}.

The gas-filled pneumatophore of adult siphonophore colonies is clearly a strong scatterer of certain frequencies of sound. Barham (1963) pointed out an apparent correlation between the depths of recorded deep scattering layers and concentrations of [physonect] siphonophores. Further, he noted that the gas bubble within the pneumatophores of *N. bijuga*, collected from an ascending scattering layer, was close to the resonance size at 12 kHz. These findings led Totton (1965) to speculate that siphonophores were the major causes of stratified zones of scattering throughout the oceans.

Stanton et al. (1994) demonstrated experimentally that freshly caught siphonophore pneumatophores produced strong echoes between 50 and 500 kHz in a laboratory tank (1 atm). Robison et al. (1998) used a 675-kHz sector-scanning sonar on an ROV to map the distributions of individual colonies in Monterey Bay. Their echogram revealed the presence of strong acoustic targets that were presumed to be adult individual colonies of *N. bijuga*. The median acoustical target strength of adult colonies of *N. cara* in the Gulf of Maine was –75 dB as measured with a dual-beam 420 kHz echosounder mounted on a 1-m^2 MOCNESS (Greene et al. 1998). More recently, Warren et al. (2001) mounted a pair of 24-kHz acoustic transducers on an ROV and recorded in situ TS values (mean of –62.5 dB) from adult colonies of *N. cara*. In this current study, it appears that the pneumatophores of siphonula larvae are also capable of producing relatively strong echoes because the dimensions of the small gas bubbles place them near, or within, the resonance zone at 43 kHz when the siphonulae are near the surface and at 120 kHz when they are near 100 m. The correlation between the presence of siphonulae and zones of enhanced backscatter in our echograms is consistent with our predictions that these small and otherwise inconspicuous organisms have a relatively strong acoustic signature that can account for much of the observed scattering in some depth strata.

Our forward problem calculations suggest that siphonulae present at our estimated densities could account for much of the observed scattering at all frequencies in the 4-h record from Jordan Basin. The observed and predicted patterns of scattering were derived from independent sources yet in several cases, both produced vertical scattering profiles that were similar in shape and frequently in magnitude. These forward calculations were highly sensitive to the pneumatophore diameters. Consequently, small shifts in the pneumatophore diameter could change the contribution to measured scattering by up to ~10 dB. At 120 kHz, our forward calculations substantially overestimated the measured scattering. The reasons for this overestimation are probably a combination of pneumatophore measurement errors and overestimation of their abundances. The pneumatophores on our VPR images were present as dark objects defined primarily by the reflection of the strobe on the surface of the pneumatophore. The relatively low resolution of the images combined with difficulty in determining the precise boundaries of the pneumatophore likely contributed to measurement error. Although we are confident that our overall estimates of the dimensions of the pneumatophores are reasonable, because measurements of preserved siphonula pneumatophores collected in a MOCNESS tow from Jordan Basin produced a similar mean diameter to the mean VPR-derived diameter, small errors in the dimensions of individual pneumatophores could drastically alter our prediction of acoustic scattering.

Our abundance estimates of the numbers of siphonulae per cubic metre were scaled up from relatively small volumes of water surveyed by the VPR. Consequently, small changes in the numbers of siphonulae imaged by the VPR could result in large changes in their abundance per cubic metre. Better estimates of both the pneumatophore dimensions and the abundances of siphonulae are certainly needed to improve our ability to predict individual components of observed scattering. However, the estimates of siphonula densities from the VPR are supported by the correspondence between predicted and observed scattering at most frequencies, given the caveats mentioned earlier about the sensitivity of our predictions near 120 kHz. That our system is so sensitive to changes in the scattering properties of siphonulae is cause for both concern and optimism. Concern, because until we have survey systems capable of collecting quantitative, high-resolution images of larger volumes of water, we may not be able to predict the contribution by organisms such as siphonulae to measured scattering with better precision. We are also optimistic, in part because imaging systems capable of higher optical resolutions and larger sample volumes are being developed, but primarily because the sensitivity of scattering calculations to pneumatophore dimensions, pressure, and acoustical frequency means that it may well be possible to extract biologically meaningful information from our echograms given appropriate "sea-truth".

It is unlikely that the enhanced acoustical scattering in the vicinity of the siphonulae strata was the result of scattering from other zooplankton. The zooplankton composition of the water column in Jordan Basin appeared similar to that of the other basins with high densities of small copepods near the surface and larger copepods, primarily *Calanus finmarchicus*, below 150 m. Strong scatterers such as thecosomate pteropods, adult siphonophores, and euphausiids were not abundant at mid-depths and were generally distributed either near the surface or below 150 m. Thus, siphonulae shared the mid-depth region with relatively few other mesozooplankton potentially capable of producing strong acoustic returns. Other organisms such as larval fish may also contain a gas inclusion with similar acoustic properties to siphonophore pneumatophores. It is unlikely that fish larvae were responsible for the observed scattering during our study because reproductive activity of fishes in the Gulf of Maine is relatively less frequent during late fall and early winter compared with other times of the year (Sherman et al. 1987) and because fish larvae in our samples were associated with surface waters, whereas most siphonulae were concentrated at mid-depth. A MOCNESS tow collected at night on 7 December (day 341) in Jordan Basin contained few fish and those that were collected were only present near the surface at a density of ~1 m^{-3}. The spatial separation of siphonulae from other targets with similar scattering properties suggests that acoustical frequencies near the resonance zone might be used to survey their distributions when a priori information confirming the absence of other gas-filled targets such as larval fish is available.

We recognize that our data set consists of a relatively small sample size of 175 siphonulae from a large area of the coastal ocean. Although our conclusions would certainly be more robust given a more complete picture of the distribution of these organisms, our VPR survey appears to be the only nonanecdotal description published thus far of the distribution of siphonulae. Our automatic image processing system was capable of detecting approximately 37% of individuals recorded by the VPR. This bias raises the question of how representative our distributional data are given that not all individuals that were present were actually detected. We are confident that the distributional patterns based on the image processor were representative of the true distributional pattern. Comparisons of siphonulae that were detected by visual examinations with image processor detections revealed similar distributional patterns that differed only in the numbers of animals present in patches and the omission of sparse patches by the image processor. Advances in image processing software for the VPR are under development to improve identification (Tang et al. 1998) and extraction efficiency; however, even without such improvements, the VPR remains one of the few tools currently capable of documenting the fine-scale distributions of these enigmatic organisms.

In conclusion, this is the first published account of the in situ biology of physonect siphonulae. In this study, we have demonstrated significant evidence of the spatial and temporal variability and environmental conditions associated with siphonulae using an advanced oceanographic survey system that appears well suited for censusing fragile gelatinous organisms. There was evidence that the gas inclusion provided buoyancy control because siphonulae occupied relatively narrow depth strata and the pneumatophore diameter (and hence volume) appeared to be constant with depth. In addition, there was correlation between the presence of siphonulae and our measured acoustic data at all frequencies. This observation was consistent with theoretical predictions of scattering. Finally, the promise of acoustic detection of these small fragile organisms was demonstrated.

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Appendix A. Estimation of pneumatophore target strength

The target strength (TS) is defined in terms of $f_{\text{pneumatophore}}$ by the relationship $\text{TS} = 10\log_{10}|f_{\text{pneumatophore}}|^2 = 10\log_{10}\sigma_{\text{bs}}$. The units of TS are dB relative to 1 m^2, and σ_{bs} (m^2) is the backscattering cross section. In fact, $f_{\text{pneumatophore}}$ is a complex function of the pneumatophore radius, the acoustic frequency, the density contrast ($g = \frac{\rho_{\text{pneumatophore}}}{\rho_{\text{water}}}$) and the sound velocity contrast ($h = \frac{c_{\text{pneumatophore}}}{c_{\text{water}}}$) between the gas in the pneumatophore and the surrounding water.

The influence of the linearly increasing water pressure with depth, which has a direct influence on the density and sound speed contrasts between the gas in the pneumatophore and the surrounding water, was included in the scattering model using the following approach (Medwin and Clay 1998). The depth dependence of the ambient water pressure is given by $p_z = p_0 + \rho_0 g z \approx (1 + 0.1z)$ atm, where p_0 is the sea level atmospheric pressure ($p_0 = 1$ atm), g is the acceleration due to gravity ($9.8\ \text{m}\cdot\text{s}^{-2}$), ρ_0 is the water density ($1030\ \text{kg}\cdot\text{m}^{-3}$), which was assumed constant throughout the water column, and z is the depth. It was assumed that the pressure, $p_{\text{pneumatophore}}$, of the gas in the pneumatophore had to equal the external water pressure (ignoring effects due to surface tension) and that the gas in the pneumatophore was an ideal gas at constant temperature. In addition, as is discussed in greater detail in the main text, there was no apparent depth dependence to the radii of the measured pneumatophores. As a result, the volume of gas (V, which contains n moles of gas of molecular weight M) in the pneumatophore was assumed constant as a function of depth. This observation of constant pneumatophore volume, combined with the assumption of an ideal gas at constant temperature (T), implies that the density of the gas increases in an amount proportional to the increase in the water pressure (ideal gas law: $p_{\text{pneumatophore}}V = nRT$, which is equivalent to $p_{\text{pneumatophore}} = \rho_{\text{pneumatophore}}RT$, where R = universal gas constant = MR, and R is the gas constant for air). Thus, the density contrast between the pneumatophore gas and the surrounding water at depth z was estimated by $g = g_0(1 + 0.1z)$, where $g_0 = 0.0012$ is the density contrast between the pneumatophore and the surrounding water at the surface (Warren 2001). Although the pneumatophore is filled with CO, the properties of air were used as an approximation.

The effect on the sound speed contrast resulting from the increasing water pressure with depth can also be estimated. For an ideal gas (Morse and Ingard 1986, p. 228) at constant volume and temperature, the sound speed of the gas in the pneumatophore is equal to the square root of the pressure over the density, $c_{\text{pneumatophore}} = \sqrt{\frac{p_{\text{pneumatophore}}}{\rho_{\text{pneumatophore}}}}$. Because the pressure is proportional to the density at all depths, the sound speed in the gas is constant. With the additional assumption that the sound speed variation of the water is small as a function of depth, it can be concluded that, to first order, the variation in the sound speed contrast, h, with depth is small. Consequently, h was taken to be constant throughout the water column, using a value of 0.22 (again, for air) taken from Warren (2001).

Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics

A.J. King, P. Humphries, and P.S. Lake

Abstract: Floodplain inundation in rivers is thought to enhance fish recruitment by providing a suitable spawning environment and abundant food and habitat for larvae. Although this model has not previously been tested in Australian rivers, it is often extrapolated to fishes of the Murray-Darling Basin. Fortnightly sampling of larvae and juveniles was conducted in the unregulated Ovens River floodplain during spring–summer of 1999 (non-flood year) and 2000 (flood year). The only species that increased in larval abundance during or shortly after flooding was an introduced species, common carp (*Cyprinus carpio*). Additionally, the peak abundance of larvae on the floodplain occurred during a rapidly declining hydrograph under low flow conditions in isolated billabongs and anabranches. The low use of the inundated floodplain for recruitment contradicts previous models. We propose a model of the optimum environmental conditions required for use of the inundated floodplain for fish recruitment. The model suggests that the notion of the flood pulse alone controlling fish recruitment is too simplistic to describe all strategies within a system. Rather, the life history adaptations in the fauna of the system and aspects of the hydrological regime such as duration and timing of inundation will control the response of a river's fish fauna to flooding.

Résumé : L'inondation de la plaine de débordement d'une rivière augmente, croit-on, le recrutement des poissons en procurant un habitat adéquat pour la fraye, ainsi que de la nourriture et un habitat pour les larves. Bien que ce modèle n'ait jamais été éprouvé en Australie, il est souvent appliqué au poissons du bassin hydrographique du Murray-Darling. Nous avons procédé à des échantillonnages des larves et des jeunes poissons à toutes les deux semaines dans la plaine de débordement de l'Ovens, une rivière qui n'est pas contrôlée par des barrages, au printemps et en été 1999 (année sans crue) et 2000 (année de crue). Une seule espèce a vu l'abondance de ses larves augmenter durant ou peu après l'inondation et c'est la carpe commune (*Cyprinus carpio*), une espèce introduite. De plus, l'abondance maximale des larves sur la plaine de débordement s'est produite pendant une période de récession du niveau de l'eau dans des conditions de débit faible dans des billabongs et des anabranches. La faible utilisation de la plaine de débordement inondée pour le recrutement contredit les modèles antérieurs. Nous proposons un modèle qui décrit les conditions optimales du milieu requises pour l'utilisation de la plaine de débordement inondée pour le recrutement des poissons. Le modèle montre que la notion de vague d'inondation qui contrôle seule le recrutement des poissons est trop simpliste pour décrire toutes les stratégies dans un tel système. Ce sont plutôt les adaptations des cycles biologiques de la faune du système et les caractéristiques du régime hydrologique, tels que la durée et la phénologie de l'inondation, qui vont contrôler les réactions de la faune des poissons d'une rivière aux inondations.

[Traduit par la Rédaction]

Introduction

The interaction of a river and its floodplain is critical for the maintenance of a river's ecological, geomorphological, and hydrological integrity (Junk et al. 1989; Poff et al. 1997). The flood pulse concept (FPC; Junk et al. 1989) postulates that the bulk of a river's productivity is derived from within the floodplain and not from downstream transport as proposed by the river continuum concept (Vannote et al. 1980). The FPC also suggests that predictable inundation of a river's floodplain is the major driving force for the maintenance of biotic diversity and the production of plant and animal biomass, including fish (Junk et al. 1989). The role of the floodplain environment in the ecology of riverine fish is emphasised, suggesting that the floodplain provides a suitable spawning environment and (or) an abundance of food

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for all life stages and is critical for the overall production of riverine fish (Junk et al. 1989; Bayley 1991).

Flooding indeed is the major cue for breeding of most riverine fish in tropical rivers throughout the world where marked seasonal differences in temperature do not occur (Welcomme 1985). In temperate systems, however, the FPC stresses the importance of the coincidence of rising temperatures and high flows for successful fish recruitment (Junk et al. 1989) (where recruitment is defined as the survival of a fish to a reference time in the life cycle (Trippel and Chambers 1997)). Thus, good recruitment should occur in situations when the rise in water level and temperature are coupled, and conversely, poor recruitment should occur if the flood either doesn't occur or retreats too quickly during spring or summer. The importance of the timing and duration of floods has been demonstrated in a number of temperate floodplain rivers (e.g., Finger and Stewart 1987; Galat et al. 1998; Sparks et al. 1998). From studies in the Mississippi River system, both Galat et al. (1998) and Sparks et al. (1998) stressed the benefit of long periods of floodplain inundation that occur when water temperatures are appropriate for spawning of native fish species.

The relationship between flooding and fish recruitment as proposed under the tenets of the FPC has been extrapolated to the Murray-Darling Basin in Australia, primarily supported by early aquaculture studies on the breeding biology of native fish of the Basin (e.g., Lake 1967*a*). Indeed, Harris and Gehrke (1994) proposed the flood recruitment model for Murray-Darling fishes, suggesting that flooding enhances recruitment by either directly stimulating spawning, for species such as golden perch (*Macquaria ambigua*) (Lake 1967*a*), or by indirectly enhancing larval and juvenile survival by providing abundant food and habitats on the inundated floodplain for larvae (e.g., Geddes and Puckridge 1988; Lloyd et al. 1989; Schiller and Harris 2001). This second pathway suggests that species such as Murray cod (*Maccullochella peelii peelii*), which do not require floods to cue spawning, may have enhanced recruitment during flood years primarily because of an increase in available food.

Despite the perceived importance of flooding for the maintenance of the Murray-Darling Basin's fish fauna, the validity of some of the assumptions behind the flood recruitment model have recently been questioned (see review Humphries et al. 1999). For example, few studies have recorded larvae or juveniles of any species using temporary floodplain habitats. Additionally, Gehrke (1990*a*, 1990*b*, 1991) and Gehrke et al. (1993) in a series of experiments concluded that although golden perch larvae were attracted to chemical leachates of river red gum (*Eucalyptus camaldulensis*), a common riparian tree, the leachates can sometimes occur in lethal concentrations in the natural environment and also that poor water quality on the floodplain may control the distribution of larvae rather than the abundance of food. Recent work has also demonstrated that many species are able to regularly spawn and recruit within the main channel, even during low flow periods (Humphries et al. 2002). Furthermore, the Murray-Darling Basin is not homogeneous climatically, and the relationship between fish recruitment and flooding may indeed vary among different climatic regions of the Basin (Humphries et al. 1999).

This study aims to determine which species use the floodplain as larvae and subsequently recruit during flood and non-flood years in an unregulated river in the southern region of the Murray-Darling Basin. Specifically, we examine the timing of spawning relative to flood events and the abundance and composition of the larval fish community during both floodplain connection and isolation. We also critically evaluate the environmental requirements for the usefulness of the floodplain as a habitat and spawning environment for the early life stages of fish.

Materials and methods

Study site

The study was conducted at one site in the lowland reaches of the Ovens River in northeast Victoria, Australia, at Peechelba in the Lavis Bend State Forest (Fig. 1). The Ovens River rises in the alpine region of Victoria and flows 150 km north where it joins the Murray River at a diversion weir, Lake Mulwala. Flooding occurs seasonally during winter–spring in most years, triggered by a combination of heavy rainfall and snowmelt. The River has a mean annual discharge of 1620×10^9 L and is one of the last remaining unregulated rivers in the southern region of the Murray-Darling Basin. The study site is an open river red gum forest that has been previously mildly logged and is still used for cattle grazing under lease arrangement. The floodplain consists of a large number of permanent and temporary billabongs (oxbow lakes) and anabranches that vary in their morphology, size, depth, and vegetation cover.

Sampling

Sampling was conducted fortnightly from September to December 1999 and 2000, a total of six and seven sampling trips, respectively. During the 1999 sampling season, the river broke its banks briefly (3 days) in early September and remained within its banks through the rest of the period (Fig. 2*a*). In 2000, three more protracted (19, 16, and 6 days, respectively) and higher floods occurred during the study period (Fig. 2*b*), with the largest flood occurring in late October. Flow data, including historical records, were supplied by Thiess Environmental Services Pty Ltd. (Woori Yallock, Victoria, Australia).

Sampling was stratified by three habitat types on the floodplain: billabongs, anabranch, and the floodplain proper. Billabongs were defined as permanent (>4 month duration), generally lentic water bodies, often containing a variety of aquatic macrophytes, with an obvious vegetative boundary and shape. Anabranches were easily distinguished from the other habitats, as they were deeper, steeper sloped, and generally had flowing water. Anabranch samples were taken at random locations at least 500 m apart along one anabranch line running through the State Forest. Floodplain proper habitats were defined as temporary (<1 month) lentic water bodies that generally contained flooded terrestrial vegetation and had no obvious boundaries. Because of the temporary nature of these habitats, their sampling was restricted to flooded or recently flooded areas. The edge of the anabranches and potential billabongs were identified and marked using tape and reflectors attached to trees during low flow times for ready identification during high flow conditions. All sampling locations were randomly selected depending on availability of

Fig. 1. (*a*) Map of the Murray-Darling Basin, Australia, showing the three broad climatic zones (after Young 2001): mountainous eastern highlands (hatched) region with cool, wet, humid climate; northern Darling River basin dominated by sporadic summer rainfall; southern Murray River basin dominated by regular winter rainfall. (*b*) Map of the Ovens River catchment in northeast Victoria, Australia.

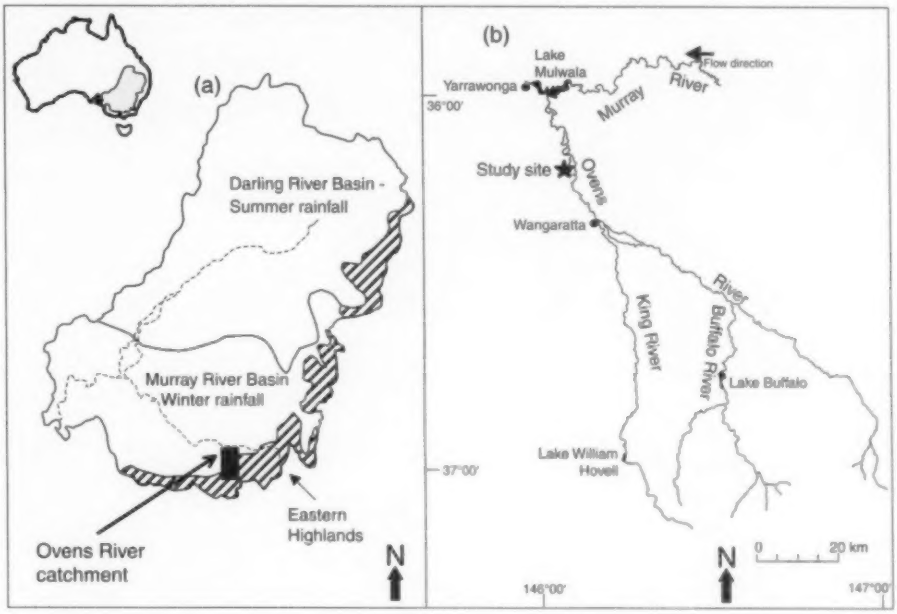
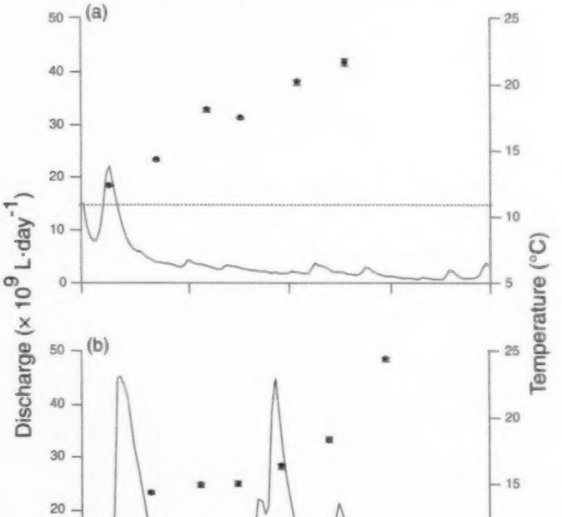

(a)
Darling River Basin - Summer rainfall
Murray River Basin Winter rainfall
Eastern Highlands
Ovens River catchment
N
(b)
Lake Mulwala
Yarrawonga
Flow direction
Murray River
36°00'
Study site
Ovens
Wangaratta
River
King River
Buffalo River
Lake Buffalo
Lake William Hovell
37°00'
0 20 km
N
146°00'
147°00'

Fig. 2. Mean daily discharge (solid line) for the Ovens River at Peechalba and mean ± standard error water temperature (solid circles) of all sampled floodplain habitats during September to January (*a*) 1999 and (*b*) 2000. Floodplain inundation occurs at 15×10^9 L·day^{-1} (broken line).



the habitat type within a 4-km^2 region within the Lavis Bend State Forest.

Sampling was conducted by three methods; however, most sampling was conducted using a new method, the sweep net electrofishing (SNE) method, which has proved effective in capturing larval and juvenile fish (King and Crook 2002). Briefly, the SNE method is a standard backpack electrofisher (model 12; Smith-Root Inc., Vancouver, Wash.) with a 15 cm diameter anode fitted with a moulded plastic rectangular frame and an attached 250 µm mesh sampling net attached to the bottom of the anode pole. The SNE method has the advantage of stunning small-bodied fish and then immediately capturing them in the fixed net (King and Crook 2002). Sampling involved approaching the selected habitat quietly, activating the anode, and moving at a constant speed in a forward zigzag motion to cover all available depths of the habitat. Sampling was divided into two 10-s periods, allowing the operator to move to a different position between periods within the habitat, reducing the potential problem of herding fish. The SNE method was used to sample shallow (≤1.0 m depth) microhabitats in billabongs, anabranches, and the floodplain proper.

A hand-trawl net was used to sample the surface of deep-water (>1.0 m) habitats, in billabongs and anabranches only. The hand-trawl net was similar in shape to a standard zooplankton sampling net, with a 30 cm diameter opening and 250 µm mesh net, tapering to a removable collection jar. The net was thrown out to the full length of an attached 5-m rope and then quickly pulled through the top of the water column. One replicate sample consisted of five pooled 5-m trawls. Drift nets were used to sample faster flowing water where drifting larvae may have occurred. Drift nets were 1.5 m long with a 0.5 m diameter mouth opening and were con-

Table 1. Minimum, maximum, and mean (±1 standard error (SE)) of water quality attributes measured during the 1999 and 2000 sampling periods.

		1999			2000		
Parameter	Units	Minimum	Maximum	Mean (SE)	Minimum	Maximum	Mean (SE)
Turbidity	NTU	15.00	155.00	73.67 (9.22)	35.00	300.00	118.24 (20.72)
Conductivity	$mS\cdot cm^{-1}$	0.04	0.09	0.06 (0.00)	0.04	0.18	0.06 (0.01)
pH		5.28	6.94	6.30 (0.13)	5.84	6.97	6.54 (0.06)
Temperature	°C	12.50	24.00	17.67 (0.92)	10.20	25.50	16.49 (0.94)
Dissolved oxygen	$mg\cdot L^{-1}$	1.60	9.90	6.76 (0.64)	0.70	9.22	6.34 (0.51)

Note: NTU, nephelometric turbidity units.

structed of 500 μm mesh, which tapered to a removable collection jar. A flow meter (model 2030R; General Oceanics Inc., Miami, Fla.) was fixed in the mouth of the net to determine the volume of water filtered. One drift net was placed in fast-flowing water in both the anabranch and main channel of the river for 3 h during the day (1300 to 1600) and 3 h at night (2000 to 2300). However, as 24-h drift sampling was not possible during this study, the peak number of drifting larvae may have occurred outside these sampling hours. Drift net samples were collected during both the day and night to collect known diel drifting species, e.g., Murray cod (King 2002).

Ten hand-trawl and 10 SNE samples were taken for each habitat type (billabongs, anabranch, and floodplain proper). However, when either flooding hindered full access to the floodplain or floodplain proper habitats had dried up, the number of samples was necessarily reduced. Therefore, because of the lack of flooding in 1999, only 10 and five SNE samples were collected in floodplain proper habitats on 9 and 23 September trips, respectively. In 2000, restricted floodplain access occurred during one major flood period, and sampling effort on 30 October was regrettably reduced to four billabong, five anabranch, and eight floodplain proper samples for each of SNE and hand-trawl sampling methods. As the result of practical considerations, sampling with the SNE and hand-trawl methods was restricted to daylight hours only and generally occurred between 1000 and 1600.

Dissolved oxygen concentration and water temperature were recorded at the location of each sample using a Horiba™ U10 water quality checker (Horiba Ltd., Japan). Turbidity, conductivity, and pH were also measured using the Horiba™ at three randomly selected sampling points on each sampling trip. Only dissolved oxygen and temperature, showing consistent patterns among either trips or habitats are presented, whereas overall mean and range of all variables have been presented (Table 1).

Preservation and laboratory methods

All samples were preserved in 95% ethanol and returned to the laboratory. Fish were sorted and identified using a dissecting microscope. Identifications were made using published (Lake 1967*b*; McDowall 1996; Neira et al. 1998) and unpublished descriptions of larvae (P. Humphries, unpublished data) and by collecting successive larval stages. Most larvae could be identified to species; however, the taxonomy of carp gudgeons (*Hypseleotris* spp.) is currently uncertain (Bertozzi et al. 2000) and therefore they are treated here as a species complex. Standard lengths of fish <10 mm were measured using an eyepiece graticule, and fish >10 mm were measured using vernier calipers, all to 0.1 mm. Fish were divided into three categories: newly hatched larvae (larvae either still retaining yolk sac or absence of flexed notochord), total larvae (individuals without full complement of fins and fin rays developed, including newly hatched larvae), and juvenile/adult (rays in all fins fully developed). Gambusia larvae (*Gambusia holbrooki*), which are born live, were classified as newly born if pelvic fin buds were absent.

Data analysis

Differences between water temperature and dissolved oxygen concentrations between the two sampling years were analysed using a three-way analysis of variance (ANOVA) model with year, trip, and habitat as fixed factors. To create a balanced design, only the first six sampling trips in 2000 were used in the analysis, and floodplain habitats were excluded. Within each sampling year, water temperature and dissolved oxygen differences among all habitats and sampling trips were established using two-way ANOVA. Post hoc examination was conducted using Tukey's test. Dissolved oxygen concentrations were converted to percent saturation and arcsine transformed before analysis. The data were checked for homogeneity of variances by examining probability plots compared with normal distributions in SYSTAT™ (SPSS Inc.), but water temperature data did not require transformation.

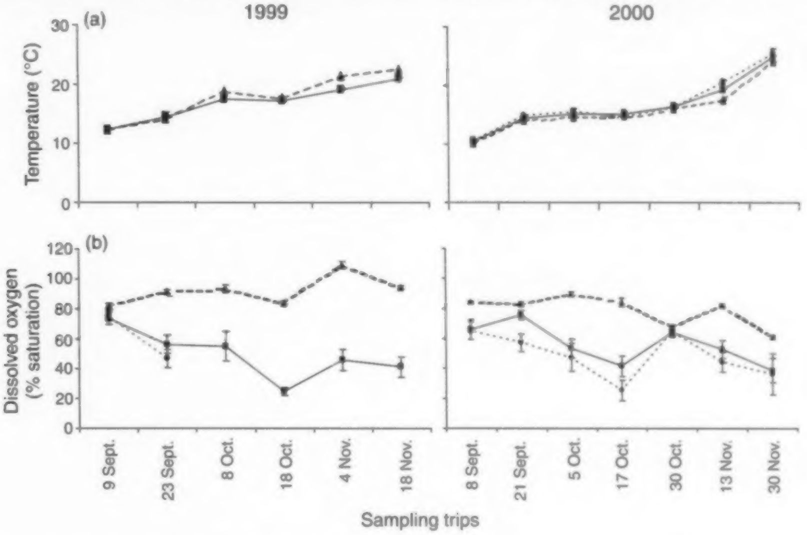
The initial description of the fish captured during sampling is presented as raw data. All other comparisons are adjusted for different sampling efforts to a standard 10 samples of the three habitat types for both the SNE and hand-trawl methods for each sampling trip. The number of larvae collected in day and night drift samples was combined for each habitat type and sampling trip and standardised to the number of larvae per 1000 m^3 of filtered water. Only five species (common carp (*Cyprinus carpio*), Australian smelt (*Retropinna semoni*), European perch (*Perca fluviatilis*), carp gudgeons, and gambusia) were collected in sufficient numbers in both years to determine their response to different flow heights. Spearman's rank correlation tests were conducted on the total abundance of all larvae and the average daily discharge on the sampling date, 1, 2, and 3 weeks before the sampling date.

Results

Water temperature and dissolved oxygen

Water temperature differed significantly between years and among sampling trips (Fig. 3*a*; $P < 0.001$). Water tem-

Fig. 3. Mean ± standard error (*a*) water temperature and (*b*) percent dissolved oxygen saturation for 1999 and 2000 sampling trips in billabong (squares, solid lines), anabranch (triangles, broken line), and floodplain proper (circles, dotted lines) habitats.



perature was significantly higher during 1999 than in the 2000 sampling period ($P < 0.001$) and increased throughout both the 1999 and 2000 study periods. There was no significant difference between habitat types overall; however, there was a significant interaction effect between year and habitat ($P < 0.001$). In 1999, temperature was on average higher in anabranch habitats than in billabongs ($P < 0.001$), whereas this pattern was reversed in 2000, where billabong and floodplain proper habitats were slightly warmer than anabranch habitats ($P < 0.001$). There was no significant difference between the water temperatures in the floodplain proper and billabongs during the 2000 sampling period ($P > 0.05$).

Overall differences in dissolved oxygen saturation were mostly explained by differences among habitat types (Fig. 3*b*; $P < 0.001$). In both years, dissolved oxygen saturation was significantly higher in anabranch than billabong and floodplain proper habitats ($P < 0.001$), whereas the dissolved oxygen saturation between floodplain proper and billabong habitats remained similar ($P > 0.05$). Dissolved oxygen saturation varied significantly through time and across habitat types during both 1999 and 2000 ($P < 0.001$). Although there was no significant difference in dissolved oxygen saturation between sampling years overall, it was significantly higher in billabong habitats in 2000 than in the previous year ($P < 0.001$) but did not differ in anabranch habitats between the two years ($P > 0.05$).

Fish community composition

A total of 1263 larvae and 504 juveniles/adults from six species and 1609 larvae and 331 juveniles/adults from 11 species were captured in the floodplain environment in 1999 and 2000, respectively (Table 2). In 1999, only four species were collected as both larvae and juveniles/adults, whereas in 2000, six species were captured as both larvae and juveniles/adults. An additional five species (mountain galaxias (*Galaxias olidus*), Murray jollytail (*Galaxias rostratus*), southern pygmy perch (*Nannoperca australis*), Murray cod, and oriental weatherloach (*Misgurnus anguillicaudatus*)) were caught as larvae in 2000. However, little information about their spawning preferences could be inferred, as they were caught in very low numbers (≤ two individuals each).

The species composition of larvae captured by both the SNE and hand-trawl methods on the floodplain differed between the two years and among sampling trips (Fig. 4). Australian smelt larvae dominated most trips in 1999, except the last sampling trip, which was dominated by carp gudgeons (Fig. 4*a*). In 2000, Australian smelt larvae dominated only the first four sampling trips, with the larvae of common carp dominating the 30 October and 13 November 2000 sampling trips and carp gudgeons again dominating the final sample in late November (Fig. 4*b*). European perch larvae were collected relatively early in both sampling years, whereas gambusia larvae were collected late in each sampling year.

Larval abundance and river flow

The total abundance of larvae captured in the floodplain environment did not correlate with simultaneous or lagged (1, 2, or 3 weeks) discharge in either 1999 or 2000 sampling seasons (Figs. 2 and 5*a*; Spearman's rank tests, $P > 0.05$). A similar number of larvae were captured from late September to late November in 1999 while the hydrograph was declining and flows were well within the banks (Fig. 5*a*). In 2000, the peak abundance of total larvae, dominated by newly hatched carp gudgeon larvae (Fig. 5*e*), occurred ~1 month after the highest peak in the hydrograph, ~2 weeks after the last over-bank flow, and coincided with a declining hydrograph and within-channel flow conditions.

The occurrence of larvae of the five main species was similar between the two sampling years (Fig. 5). The total abundance of common carp larvae was generally higher in 2000 than in 1999 (Fig. 5*b*). Newly hatched common carp larvae occurred throughout the sampling period in both

Table 2. Number of larvae and juvenile/adults of each species captured in 1999 and 2000 between habitat types (main channel (Mch),

			1999					
			Mch	Ana			BB	
Common name	Stage	Length (mm)	Drift	Drift	SNE	HT	SNE	HT
Common carp (*Cyprinus carpio*)*	Larvae	3.8–18.9	2(28)		58	3	138	10
	Juveniles	14.1–46.6			1		15	
Australian smelt (*Retropinna semoni*)	Larvae	4.1–20.2			42	148	18	578
	Juvenile/adults	18.4–51.0		2(3)			2	34
European perch (*Perca fluviatilis*)*	Larvae	5.6–11.6	5(2)	5(10)	4			2
	Juveniles	21.6–31.7						
Carp gudgeons (*Hypseleotris* spp.)	Larvae	1.7–11.2			3	30	3	167
	Juvenile/adults	11.5–39.9	3(77)	6(17)	219	2	5	2
Gambusia (*Gambusia holbrooki*)*	Postlarvae	6.2–12.9					45	1
	Juvenile/adults	8.0–41.7			18		171	20
Flathead gudgeon (*Philypnodon grandiceps*)	Juvenile/adults	30.1–48.2			2		1	
Mountain galaxiid (*Galaxias olidus*)	Larvae	12.4–13.0						
	Juveniles	24.2						
Murray jollytail (*Galaxias olidus*)	Larvae	10.4–11.6						
Southern pygmy perch (*Nannoperca australis*)	Larvae	8.1						
Murray cod (*Maccullochella peelii peelii*)	Postlarvae	10.1						
Oriental weatherloach (*Misgurnus anguillicaudatus*)*	Juveniles	25.5						
Total larvae			7(30)	5(10)	10 718	1	20 475	8
Total juvenile/adult			3(77)	8(20)	240	2	194	56
Total fish			10(107)	13(30)	34 718	3	39 881	4
No. samples			12	6	60	60	60	60
No. fish·sample^{-1}			0.83	2.17	5.78	3.05	6.63	13.6

Note: All data are presented as unadjusted raw data. Standardised drift abundance (number·1000 m^{-3}) shown in parentheses. An asterisk (*) indicates

years; however, their abundance peaked during the late October flood event in 2000. Two major peaks in the abundance of newly hatched Australian smelt larvae occurred in late September and late October 1999, but only one peak was observed in early October in 2000, followed by a decline during and after the late October flood in 2000 (Fig. 5*c*). European perch larvae were first recorded in early to mid-September in both years, when temperatures were relatively cool, but only in low numbers (Fig. 5*d*). Carp gudgeon larvae were first collected in mid-October in 1999 but not until mid-November in 2000 (Fig. 5*e*). Similarly, gambusia postlarvae were first collected in early November in 1999 but not until early December in 2000 (Fig. 5*f*).

Discussion

Occurrence of larvae on the floodplain

Floodplain habitats have been demonstrated to be important nursery areas for larval and juvenile fishes in large floodplain rivers (e.g., Welcomme 1985; Turner et al. 1994; Killgore and Baker 1996). Some fishes undergo migrations from the main river channel to use temporarily inundated habitats for spawning and feeding (Goulding 1980; Ross and Baker 1983; Poizat and Crivelli 1997), whereas others reside and recruit in a range of permanent and semi-permanent habitats such as off-channel lakes (billabongs) and anabranches (Copp 1989). Of the 19 fish species known to occur in the Ovens River system, we collected larvae of only five species in sufficient numbers to indicate widespread spawning and direct use of the floodplain environment. These species included two native (Australian smelt and carp gudgeons) and three introduced (European perch, common carp, and gambusia) species. An additional five species were recorded in very low numbers only in 2000 (flood year). Importantly, all five common species occurred as larvae during both the non-flood and flood years, suggesting that spawning and recruitment of these species is not reliant on floodplain inundation and use of temporary floodplain habitats, but can occur in isolated, more permanent billabongs and anabranches in the floodplain environment. Each of these commonly caught species can reside and recruit in the main channel of rivers and in isolated permanent billabong environments (McDowall 1996; Humphries et al. 2002). Additionally, two species in the present study, carp gudgeons and gambusia, only spawned during low flow conditions, when waters were not present on the floodplain proper, even in the high flow year. This suggests that these species may have a preference for low flow conditions for spawning and successful rearing of their young in floodplain habitats, similar to that proposed in the low flow recruitment hypothesis for main channel habitats (Humphries et al. 1999).

Despite the emphasis on the importance of flooding in the recruitment of native fish in the Murray-Darling Basin (see Humphries et al. 1999; Schiller and Harris 2001), only common carp, an introduced species, showed an increase in larval abundance during or shortly after flood periods. In addition, the peak abundance of total larvae in all floodplain habitats did not occur during flood events but during a rapidly declining hydrograph and low flow conditions. The low use of the inundated floodplain by fish larvae demonstrated in the field study presented here does not support previous studies and hypotheses on the importance of the inundated floodplain for fish recruitment (Welcomme 1985; Junk et al. 1989; Harris and Gehrke 1994). In an attempt to explain these results, we propose a model describing the optimum environmental conditions required for use of the inundated anabranch (Ana), billabong (BB), and floodplain (FL)) and three methods (drift net, sweep net electrofishing (SNE), and hand trawl (HT)).

1999		2000							
FL		Mch	Ana			BB		FL	
SNE	Total	Drift	Drift	SNE	HT	SNE	HT	SNE	Total
	211	73(2757)	48(63)	72	14	171	50	245	673
	16			2	1	19		12	34
	786	3(18)		59	80	46	346	20	554
	38	1(6)	1(1)		19	1	3		25
1	17	4(25)	2(2)	3		1	7	1	18
				1		1			2
	203	2(150)	2(13)	6	4	12	277		303
	237	3(82)	9(31)	153	2	14	2	6	189
	46			9		20	3	21	53
1	210			17		18	1	15	51
	3	2(76)	2(4)	24		1			29
					1			1	2
							1		1
			1(6)	1					2
								2	2
			1(13)						1
								1	1
1	1263	82(2950)	54(99)	150	99	25 068	3	291	1609
1	504	6(164)	12(36)	197	22	54	7	33	331
2	1767	88(3114)	66(135)	34 715	1	30 469			1940
15		13	13	65	65	64	64	63	
0.13		6.77	5.08	5.34	1.86	4.75	10.8	5.14	

introduced species.

floodplain for fish recruitment and discuss the suitability of the fish fauna in terms of their life history characteristics and environmental conditions present in the Ovens River for use of the floodplain for recruitment.

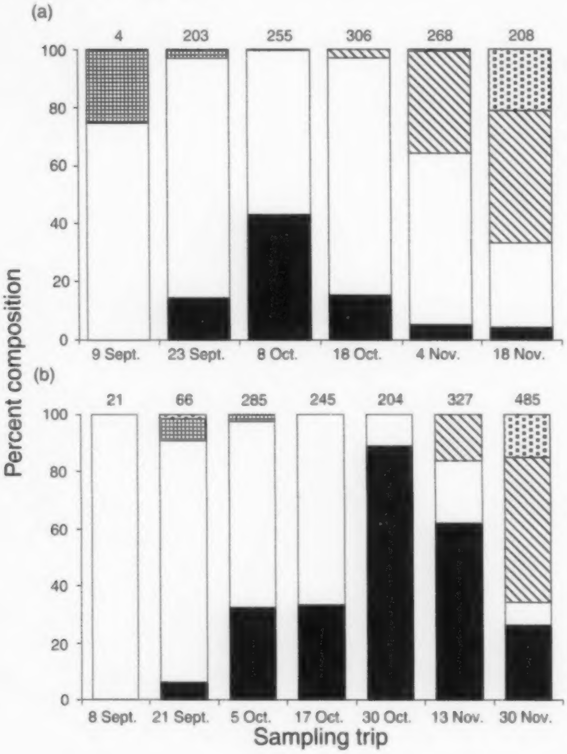
Optimum environmental conditions for use of the inundated floodplain for recruitment

The use of the inundated floodplain for fish recruitment is likely to be influenced by a number of interrelated factors, such as the degree of coupling of high flows and temperature, the predictability of the flood pulse, the rate of rise and fall of the hydrograph, the duration of the inundation period, and the amount of the floodplain that is inundated. Based on these factors, we have constructed a model that describes the optimum environmental conditions for successful fish recruitment on the inundated floodplain (Fig. 6). The supporting evidence for each of these optimum conditions is discussed below.

Generally fishes spawn during the warmest months of the year, partly because of increased growth rates when temperatures are high and partly, at least in temperate systems, because this is also the period of maximum production of food for larvae and juveniles (Jobling 1995). In tropical systems, where seasonal changes in temperature and day-length patterns are relatively small, often the major predictable seasonal event is a rise in water level which cues the spawning and movement of adult fish onto the inundated floodplain (Lowe-McConnell 1975; Welcomme 1985). In temperate systems, where the timing of spawning is more likely to be controlled by temperature and light regimes than flooding cycles, the FPC emphasised the importance of a "coupled" rise in flow and temperature in maximising the use of the floodplain for fish recruitment, as this provides the best conditions for spawning and successful rearing of their larvae (Junk et al. 1989). For example, Finger and Stewart (1987) demonstrated that timing and duration of flooding in any one year could control the dominance of spring versus summer spawning species in the fish community. Sparks et al. (1990) suggested that any departure from this coupled condition could result in a disturbance, with a "decoupling" of high flows and temperature resulting in poor recruitment because of limited nursery areas and a reduction in food and (or) spawning sites. Thus, the first component of our model suggests that the optimum conditions for recruitment on the floodplain should occur when rises in temperature and flows coincide (Fig. 6*a*).

The FPC was primarily developed from observations of large tropical rivers where the flood pulse is highly predictable (Junk et al. 1989). The interannual predictability of floods is critical for strong fish recruitment and production in large rivers and favours the development of morphological, behavioural, and physiological adaptations of aquatic organisms to flooding (Junk et al. 1989; Bayley 1991). In an analysis of the hydrological characteristics of a number of the world's rivers, the dryland rivers of the Murray-Darling Basin and tropical rivers were found to be at the extreme opposite ends of a continuum of hydrological variability (Puckridge et al. 1998). Puckridge et al. (1998) also suggested that dryland rivers such as the Cooper and Diamantina creeks in the northern region of the Basin could be considered to be among the most variable in the world. Unpredictability does not necessarily preclude the development of adaptations to flooding, as opportunism, flexibility, and trophic generalisation could be viewed as evolutionary adaptations to a variable flow regime (Poff and Allan 1995; Walker et al. 1995; Puckridge et al. 1998). However, the

Fig. 4. Larval fish composition for (*a*) 1999 and (*b*) 2000 sampling trips. Data do not include fish captured in drift net samples and are adjusted for the different efforts between sampling trips: common carp (*Cyprinus carpio*; solid bars), Australian smelt (*Retropinna semoni*, open bars), European perch (*Perca fluviatilus*, checkered bars), carp gudgeons (*Hypseleotris* spp., diagonally hatched bars), and gambusia (*Gambusia holbrooki*, dotted bars). Number above bar indicates total number of fish collected per sampling trip.



more predictable that flooding is, the more likely it would be that the importance of flooding is incorporated into a fish's life cycle (Fig. 6*b*).

The rate of change from one flow condition to another can influence the range and strength of biotic responses to flooding (Poff et al. 1997). A slow to moderate increase in water level is likely to produce strong year classes, as fish are thought to respond to the increased production of vegetation and associated food and habitat as the moving littoral zone traverses the floodplain (Junk et al. 1989; Bayley 1991). In some systems, a rapid rise is generally followed by a rapid fall, and therefore, the flood may have little direct benefit for aquatic biota (Bayley 1991). In cases where sudden changes in the hydrograph occur, fish may be displaced downstream during sudden rises or be left stranded in isolated pools on the floodplain during the drying phase. Bonetto et al. (1969) estimated that 40 000 tonnes of fish are lost via stranding in the Parana River system every year. In the present study, large numbers of common carp larvae and juveniles were left stranded in temporary, shallow pools on the floodplain after the major flood event in October 2000 (A.J. King, personal observation). Thus, a relatively slow rate of rise and fall would be more advantageous for a species to use the floodplain for recruitment (Fig. 6*c*).

The length of time that flood waters remain on the floodplain can also dictate the strength of biotic responses to the flood (Boulton and Lloyd 1992; Poff et al. 1997). However, constant high water levels can also create areas on the floodplain with poor water quality and can reduce fish production (Junk et al. 1989). A number of studies have suggested that varying periods of inundation are critical for the optimum use of the floodplain for fish recruitment. At one end of the extreme, floodplain inundation in tropical regions commonly occurs for periods of up to 6 months (Goulding 1980; Welcomme 1985). In the Mississippi River, Sparks et al. (1998) demonstrated that slowly receding floods of 6 weeks or more were critically important for use of the floodplain for fishes, especially for those species that build nests. In Australia, although no studies have demonstrated the period required for successful use of the floodplain for fish recruitment, suggested values based on the estimated time of some native fishes from spawning to full development into juveniles range from 2 to 4 months (Geddes and Puckridge 1988; Lloyd et al. 1989; McKinnon 1997). Therefore, several weeks to several months is considered the optimum period of floodplain inundation that is required for fish to spawn and larvae to hatch and then feed and develop into juveniles (Fig. 6*d*).

Higher catches of larval fish can correspond to higher water levels because of the expansion of the aquatic–terrestrial transition zone and increased production within the forested floodplain (Killgore and Baker 1996). The amount of the floodplain under inundation may therefore influence the number of fish produced from the floodplain (Welcomme 1985; Bayley 1991) by increasing the diversity of aquatic habitats available for spawning and rearing of their young (Fig. 6*e*).

Optimum environmental conditions, life history characteristics, and likelihood of fish recruitment on the inundated floodplain in the Ovens River

For a species to gain maximum benefit from the inundated floodplain for recruitment, its spawning period should occur when high flows and high temperatures are coupled. However, the Ovens River represents a classic example of the "decoupled" scenario of Junk et al. (1989; Fig. 6*a*), with the highest mean annual flows occurring in late winter and early spring as snowmelt floods (Figs. 7*a* and 8*a*), whereas the highest water temperatures generally occur a few months later in summer. Indeed, in 26 out of 100 years, no overbank flows will occur in the Ovens River. However, of the remaining years, flooding occurs in spring about 50% of the time, but rarely in summer (Fig. 8*a*). Therefore, for summer spawning species, there is a much lower chance of flooding occurring during their spawning period (Fig. 7*b*).

Although high temperature and flow in the Ovens River are decoupled, spring spawners could perhaps benefit from the relatively predictable spring flooding. Of the 19 species known to exist in the lowland reaches of the Ovens River, five species are thought to be solely spring spawners, the remainder being either spring–summer spawners or solely summer spawners (Fig. 7*b*). Therefore, spring or spring–

Fig. 5. Abundance of (*a*) total larvae, (*b*) common carp (*Cyprinus carpio*), (*c*) Australian smelt (*Retropinna semoni*), (*d*) European perch (*Perca fluviatilus*), (*e*) carp gudgeons (*Hypseleotris* spp.), and (*f*) gambusia (*Gambusia holbrooki*) for combined sweep net electrofishing (SNE) and hand-trawl samples during 1999 and 2000 sampling trips, adjusted for the different efforts between sampling trips. Bar indicates total abundance of larvae, with the solid portion representing newly hatched larvae. A small arrowhead on the *x*-axis indicates sampling trips.

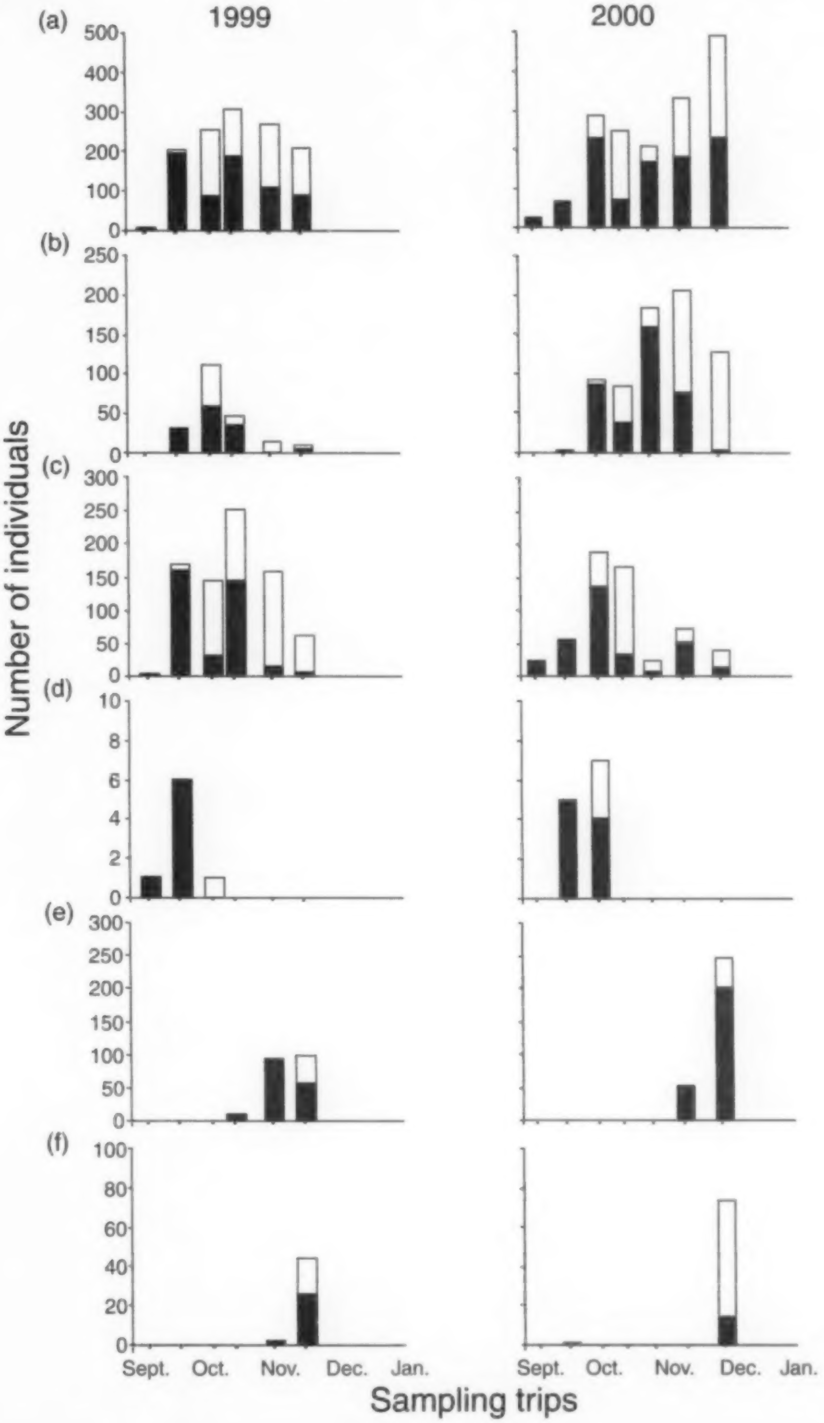
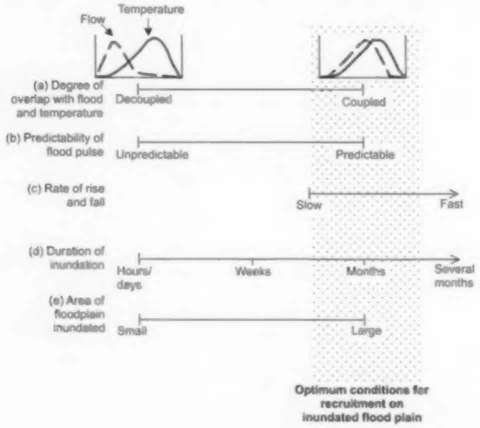


Table 3. An assessment of the likelihood of the fish fauna in the Ovens River to use inundated floodplains for recruitment based on

	Golden perch	Silver perch	Macquarie perch	River blackfish	Murray cod	Trout cod	Rainbow fish	Carp gudgeons
Overlapping spawning and flood period	N?	?	Y	Y	N	Y	N	N
Flexible spawning period	Y	Y?	N	N	N	Y	N	N
Protracted spawning period	N	N	N	N	N	N	N	N
Generalist spawning attachments	Y	Y	N	N	N	N	Y	Y
Larval drift	Y?	Y?	Y?	N?	Y	Y	N	N
Rapid early development	Y (20 days)	Y (20 days)	Y? (20 days)	N? (30 days)	N (36 days)	N? (36 days)	Y? (14 days)	Y? (14 days)
Adaptations to poor water quality	N	N	?	?	?	?	?	?
Life span (>3 years)	Y	Y	Y	Y	Y	Y	N	N
Likehood of use of floodplain for fish recruitment	Low	Low	Med.	Low	Low	Med.	Low	Low

Note: Y, yes; N, No; ?, no information or estimate; Med., medium; LB, live bearers. An asterisk (*) indicates introduced species. References: 2000; Humphries et al. 2002); generalist spawning attachments, including broad and pelagic spawners (McDowall 1996; Koehn et al. 2000); larval drift (golden perch and silver perch (Gehrke 1991); gambusia, carp, and oriental weatherloach (D. McNeil, LaTrobe University, Victoria, Australia, personal

Fig. 6. Conceptual model of the optimum environmental conditions for use of the inundated floodplain for fish recruitment.


Flow
Temperature
(a) Degree of overlap with flood and temperature
Decoupled
Coupled
(b) Predictability of flood pulse
Unpredictable
Predictable
(c) Rate of rise and fall
Slow
Fast
(d) Duration of inundation
Hours/days
Weeks
Months
Several months
(e) Area of floodplain inundated
Small
Large
Optimum conditions for recruitment on inundated flood plain

summer spawners with protracted or flexible spawning periods may benefit from any flood events in this system by using the floodplain for recruitment. Flexible spawning periods may allow a species to delay potential spawning until the right conditions are present, such as a flood, to enhance recruitment success, whereas protracted spawning periods may allow at least a proportion of the young to encounter flood periods. In the Ovens River, only two native species (golden perch and silver perch (*Bidyanus bidyanus*)) are thought to have flexible spawning periods (Table 3), with the ability to delay spawning until water levels rise after a critical minimum temperature is reached (Lake 1967*a*; Mackay 1973). An additional two native species (Australian smelt and flathead gudgeon (*Philypnodon grandiceps*)) are thought to have protracted spawning periods (Table 3). However, in the present study most of the solely spring spawners or species with protracted or flexible spawning periods were either not captured at all or in very low numbers. Australian smelt was the only native species to occur in high numbers during floodplain inundation, but it was also present in low flow conditions in both years and showed no evidence of an increase in spawning or recruitment with flooding.

The frequency of flooding influences the capacity of a population to respond to flooding (Fig. 6*b*), and this will vary with the generation times of each species (Walker et al. 1995). For example, if flooding occurs irregularly, short-lived species may not live long enough to encounter suitable periods of floodplain inundation. Thus, longevity may be an advantageous life history trait for flood-dependent species, especially in systems with a low frequency of flooding. A number of species in the Ovens River are long lived (Table 3); however, the flooding patterns in the Ovens River despite being decoupled are actually fairly predictable, with flooding occurring in spring in up to 50% of years (Fig. 8*a*), and it would be unlikely to limit the use of the floodplain for recruitment to long-lived species only.

Our model suggests that for fish to successfully use the inundated floodplain for recruitment, the floodplain needs to be inundated for several weeks to months (Fig. 6*d*). In the Ovens River, nearly 60% of floods will occur for less than 10 consecutive days, and floods of more than 40 days duration are very rare (Fig. 8*b*). In these types of systems, fish may risk becoming stranded if they use the floodplain for recruitment, especially if they have specialised spawning requirements such as nest building, parental care, or slow egg and larval development periods (e.g., Murray cod, trout cod, and river blackfish (*Gadopsis marmoratus*; Humphries et al. 1999; Table 3). In tropical floodplain rivers, nest building among fishes is common (Welcomme 1985); however, the inundation period is much longer, in the order of months, rather than days as for the Ovens River. Therefore, characteristics such as generalist spawning habitat requirements (e.g., broadcast and pelagic spawning) and rapid development of young may be an advantage (Table 3).

advantageous life history characteristics.

Southern pygmy perch	Mountain galaxias	Murray jollytail	Australian smelt	Flathead gudgeon	Flyspecked hardyhead	Gambusia*	Common carp*	Goldfish*	European perch*	Oriental weather loach*
Y	Y	?	Y	Y	Y	N	Y	Y?	Y	?
Y	Y	?	N	N	N	Y (multiple broods	Y (multiple spawning)	N	Y	?
N	N	?	Y	Y	N	Y	Y	N	N	?
Y	Y	Y	Y	Y	Y	Y	N	Y	N	Y
N	N	N	Y	Y	Y?	N	Y	Y?	Y	N
Y? (14 days)	Y? (14 days)	Y? (14 days)	Y? (14 days)	Y? (14 days)	Y? (14 days)	(LB)	Y (20 days)	Y? (20 days)	N (60 days)	?
?	?	?	?	?	?	Y	Y	Y?	?	Y
N	N	N	N	N	N	N	Y	Y	Y	Y
Low	Low	Low	Med.	Med.	Low	Med.	High	Med.	Med.	Low

overlapping spawning and flood period in Ovens River, based on Fig. 7; flexible or protracted spawning period (Koehn and O'Connor 1990; Koehn et al. (Humphries et al. 2002); rapid early development, estimate of spawning to juvenile period (Lake 1967*b*; Villizzi 1998); adaptations to poor water quality communication)); life span (McDowall 1996).

Lengthy inundation of floodplain environments often results in poor water quality conditions, especially low dissolved oxygen levels and high concentrations of tannins and polyphenols (Welcomme 1985; McKinnon 1997; Fontenot et al. 2001). Thus, it would be advantageous for fishes in this environment to be able to avoid or tolerate adverse water quality conditions. Air breathing and other adaptations to low oxygen concentrations are frequently found in tropical floodplain fishes (Welcomme 1985; Junk et al. 1989). Experiments on golden perch and silver perch larvae in artificial floodplain environments demonstrated that larvae of these species actively avoided areas of low dissolved oxygen concentrations (Gehrke 1990*a*, 1991). For all other native species in the Ovens River, there is insufficient information to determine whether they exhibit any adaptations to poor water quality conditions. However, four of the five introduced species exhibit adaptations to poor water quality, including air or surface breathing (Table 3).

Recruitment on the inundated floodplain environment is commonly thought to be via two main mechanisms: either adult fish move onto the floodplain and spawn in inundated floodplain areas or their larvae and (or) juveniles drift from the main channel into the inundated floodplain (Geddes and Puckridge 1988; Harris and Gehrke 1994; Schiller and Harris 2001). This drifting strategy may allow eggs or larvae originating from the main channel to drift onto the inundated floodplain and may increase the likelihood of the species using the inundated floodplain environment for recruitment (Table 3). Although true lateral movements of larval and juvenile fish into floodplain environments have not been studied, species such as Murray cod and common carp are known to drift in main channel environments (King 2002; Humphries et al. 2002). Golden perch and silver perch are also thought to have drifting egg and larval stages (Lake 1967*a*, 1967*b*) but as yet have not been collected in large numbers in the wild. The only species collected in high numbers in drift nets in the present study was common carp, suggesting that although common carp spawning occurred directly on the inundated floodplain, some larvae were also transported from other habitats upstream onto the floodplain.

Analysis of the life history characteristics that may be advantageous for the use of inundated floodplains for recruitment suggested that most species in the Ovens River have a "low" or "medium" likelihood of using the floodplain for recruitment (Table 3). This is supported by the findings of the present study, as most of these species were not captured on the inundated floodplain. The only species occurring in the Ovens River to receive a "high" likelihood of using the inundated floodplain for recruitment was the introduced species, common carp (Table 3). This was supported by the present study in that it was the only species to demonstrate an increase in larval abundance with the major flood event in October 2000. Common carp have a number of life history characteristics that allow them to take advantage of unpredictable flood conditions. Importantly, however, common carp are known to both spawn and recruit in the main channel of floodplain rivers when flows are well within the banks (King 2002; Humphries et al. 2002).

Although golden perch and silver perch exhibit a number of the life history characteristics favourable for utilisation of the inundated floodplain (Table 3), they received an overall rating of only "low" likelihood to use the inundated floodplain in the Ovens River, primarily because flooding rarely occurs when the suggested critical minimum spawning temperature of 23°C is reached (Fig. 8). Although abundant as adults in the Ovens River, golden perch larvae were not found in the present study, presumably because flooding did not coincide with their potential breeding period. Therefore, in the southern region of the Murray-Darling Basin, where floods generally occur throughout the winter–spring period before water temperatures have risen substantially (Fig. 1*a*), the likelihood of successful recruitment of golden perch may be greatly reduced. In contrast, the northern region of the Basin tends to receive flooding of a long duration in summer when temperatures are high (Young 1999). The main factors controlling the use of the floodplain for

Fig. 7. (*a*) Mean monthly discharge (solid line) and water temperature (broken line) and (*b*) the estimated spawning calendar of most fish species known from the Ovens River. Mean monthly data were calculated from flow and temperature records at Wangaratta on the Ovens River for 1977 to 1989. Note that the carp gudgeon estimated spawning calendar is for the species complex. An asterisk (*) indicates introduced species. The spawning calendar is based on the following estimates: (1) Humphries et al. 2002; (2) King 2002; (3) Ingram and Douglas 1995; (4) Milton and Arthington 1985; (5) O'Connor and Koehn 1991; (6) Cadwallader and Rogan 1977; (7) Appleford et al. 1998; (8) Milton and Arthington 1983; (9) Llewellyn 1979; (10) Cadwallader 1977; (11) Backhouse and Frusher 1980; (12) Milton and Arthington 1984; (13) Jackson 1978; (14) Mackay 1973; (15) Llewellyn 1974; and (16) Humphries 1995.

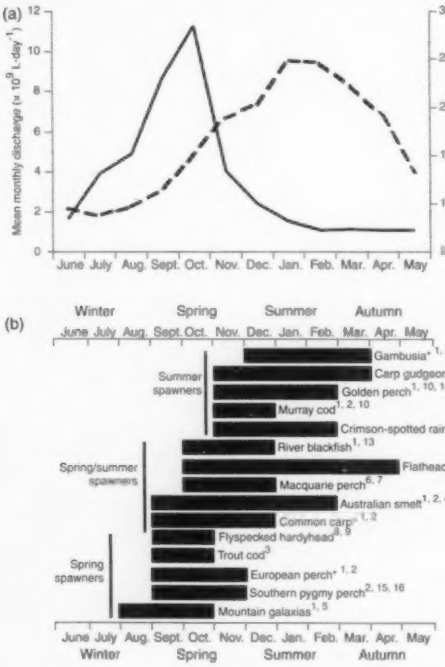
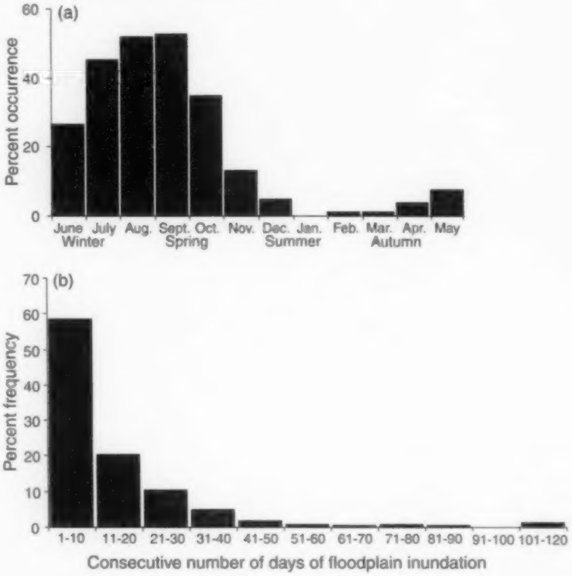


Fig 8. (*a*) Percent occurrence of floodplain inundation (>15 × 10^9 L·day^{-1} at Wangaratta) per month and (*b*) percent frequency of the number of consecutive days of floodplain inundation in the Ovens River at Wangaratta, both calculated from historical flow records from 1892 to 1997. Consecutive day calculation also includes nonflood periods of less than 10 days duration between consecutive flood events.



fish recruitment in the northern region of the Basin is likely to be the unpredictability and low incidence of flooding. However, golden perch exhibit some possible adaptations to this unpredictability (e.g., flexibility in spawning time and longevity) and may therefore successfully spawn and recruit in these environments.

In conclusion, exploration of the inundation patterns in the unregulated Ovens River compared with the predictions of the optimum environmental conditions required for use of the inundated floodplain for fish recruitment has demonstrated that most of these optimum factors rarely occur in the Ovens River system. This may also be true for other rivers in the southern winter rainfall region of the Murray-Darling Basin, especially under their natural flooding regimes. Additionally, we suggest that the number of species that will directly use the inundated floodplain for recruitment is likely to be small. The only species that appears to have favourable life history characteristics to successfully use the inundated floodplain for recruitment is common carp, an introduced species. However, even common carp are also capable of spawning and recruiting in low flow conditions on the floodplain and main channel environments. Other species (e.g., golden perch) are unlikely to use the floodplain in the winter rainfall region of the Basin but may recruit well during flood years in the north of the Basin where the timing of floods and high temperatures may be coupled.

This study suggests that the optimum environmental conditions and life history adaptations for direct use of the floodplain for fish recruitment do not necessarily occur in all floodplain rivers or for all fish species present in them. Therefore, careful consideration should be given to a river's hydrological regime and life history characteristics of the fish fauna before any conclusions regarding the importance of direct use of the floodplain for fish recruitment can be drawn. However, we are still a long way from conclusively defining the role of the floodplain in fish community dynamics. In systems where the use of the floodplain environment for spawning and recruitment is limited, such as the southern region of the Murray-Darling Basin, periods of floodplain inundation may provide valuable indirect benefits to fish recruitment, such as providing a boost of nutrients and prey items in returning waters to permanent water bodies including the main channel. Flooding also sustains and connects billabong communities, which is of obvious importance to the ecology of wetland dwelling species. Finally, this study only examined the role of overbank flows, i.e., the flood pulse, and did not examine the role of within-channel rises, i.e., the flow-pulse (sensu Puckridge et al. 1998; Tockner et al. 2000), on fish recruitment dynamics. Further work is required to elucidate the role that flooding and flow pulses may have in the ecology of fishes in floodplain rivers.

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On the distribution of the European eel (*Anguilla anguilla*) and its fisheries

Willem Dekker

Abstract: For the distribution of the European eel (*Anguilla anguilla*), only Schmidt (1909) has conducted substantial investigations, yielding a qualitative description (Atlantic and Mediterranean coasts of Europe and Northern Africa). In this article, a meta-analysis of reported fishing yields is presented, showing a major concentration of glass eel yield in the Bay of Biscay (and possibly farther south) and of yellow and (or) silver eel yield in the western Mediterranean. Fisheries target the glass eel stage at highest stock density and shift to the silver eel stage at low density. Because there is no suitable habitat in the Sahara, the southern limit is, contrary to Schmidt's belief, primarily determined by continental conditions. From the centre of the distribution to the north, a long and slow decline in density occurs. The mismatch between northern temperatures and the species' preference, in combination with the very low abundance, indicates that the European eel is best seen as a warm-water species, like most other eel species (*Anguilla* spp.), showing a considerable northern diaspora.

Résumé : Seul Schmidt (1909) a réalisé une étude de grande envergure avec des descriptions quantitatives de la répartition géographique de l'anguille d'Europe (*Anguilla anguilla*) sur les côtes atlantiques et méditerranéennes de l'Europe et de l'Afrique du Nord. On trouvera ici une méta-analyse des rendements de pêche qui montre une concentration majeure des rendements de civelles dans le golfe de Gascogne (et peut-être plus au sud) et des rendements d'anguilles jaunes et (ou) argentées dans la Méditerranée occidentale. Les pêches commerciales ciblent les civelles lorsque les densités de stock sont à leur maximum et visent plutôt le stade de l'anguille argentée aux basses densités. Puisqu'il n'existe pas d'habitat approprié dans le Sahara, la limite australe est déterminée principalement par les conditions sur le continent, contrairement à ce que pensait Schmidt. Il se produit une diminution lente et à grande échelle de la densité depuis le centre de la répartition vers le nord. La discordance entre les températures nordiques et la température préférée de l'espèce, ajoutée aux très faibles abondances, indique que l'anguille d'Europe doit être considérée comme une espèce d'eau chaude, comme la plupart des autres espèces d'anguilles (*Anguilla* spp.), qui a une importante diaspora nordique.

[Traduit par la Rédaction]

Introduction

The continent-wide distribution of the European eel (*Anguilla anguilla* (L.)) is generally considered a well-established fact. Schmidt (1909) collected information on the distribution area of the different eel species on the continents and interpreted the distribution in relation to his new insight in the oceanic life stages (Schmidt 1923). To my knowledge, this is the one and only comprehensive study of the distribution area of the European eel (Fig. 1). Since 1909, all maps of the distribution area cite Schmidt (1909) as their prime source of information. Schmidt's focus was on the outer limits of the distribution area. Although there is little doubt that eels occur within the outer limits (Tesch 1999), nothing has been published on the variation in density of the stock contained within.

The stock of the European eel is in decline. Recruitment to (Moriarty 1986; Moriarty and Tesch 1996; Dekker 2000*a*), as well as yield from (W. Dekker, unpublished data), the continental stock has been well below average for two or more decades. A stock recovery plan is urgently needed (ICES 1999). Moriarty and Dekker (1997) recommend increasing recruitment by glass eel restocking in northern areas, while assuming that recruitment in southern areas is overabundant in relation to the carrying capacity of the inland waters and can be exploited safely. A spatial differentiation in management regime is advocated, but no corresponding management regions have yet been defined.

Eels are notoriously hard to sample. Stock densities vary over short ranges in predictable (Barak and Mason 1992) and unpredictable (Dekker 2000*a*) ways, and sampling problems make reliable estimation of local stock densities problematic (Knights et al. 1996). In addition, sampling methods have not been standardised or intercalibrated (Moriarty and Dekker 1997); therefore, comparison of estimates of stock density within and between catchments and countries is not appropriate. Instead, data on commercial landings will be analysed here. Commercial landings are indicative of local stock sizes in as far as fishing takes a constant fraction, i.e., fishing mortality is constant over the distribution area. There is substantial evidence to the contrary (Moriarty and Dekker 1997; Dekker 2000*a*). However, the number of silver eels escaping to the ocean is negligible in comparison with commercial landings (Dekker 2000*b*). Variation in fishing inten-

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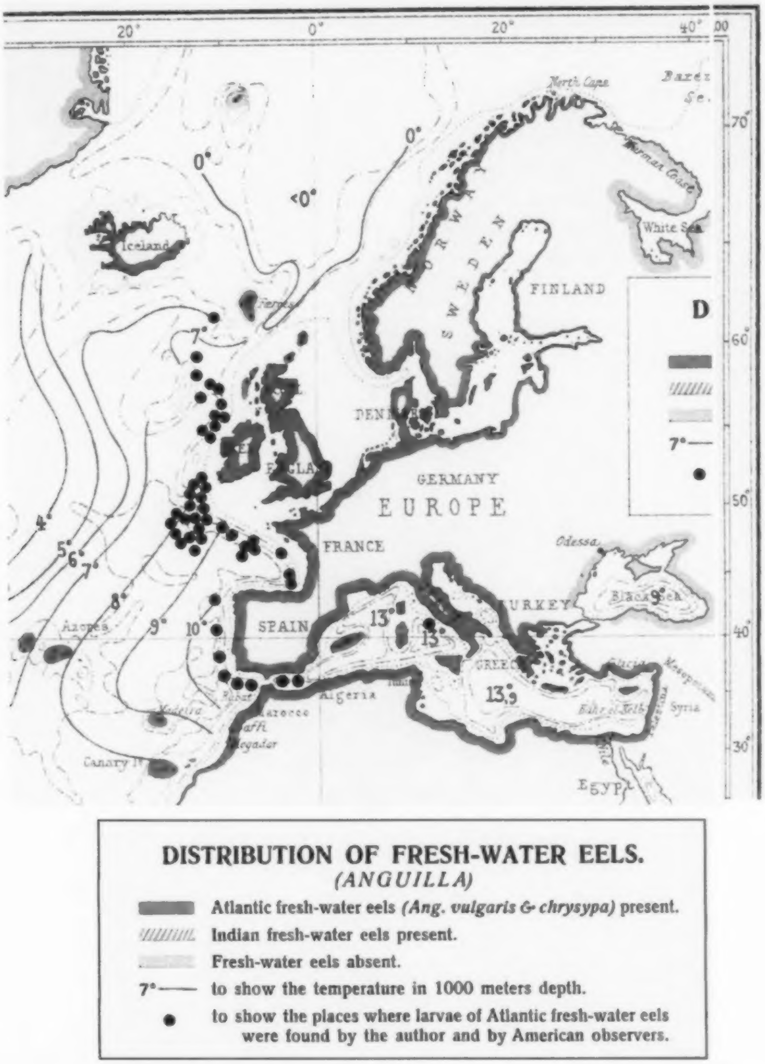
Fig. 1. Reproduction of the chart from Schmidt (1909), selecting parts relevant for the distribution of the European eel (*Anguilla anguilla*), 25–75°N and 25–40°E.


20°
0°
20°
40°
70
60
50
40
30
North Cape
Barents Sea
Murman Coast
White Sea
Iceland
Feroes
NORWAY
SWEDEN
FINLAND
DENMARK
ENGLAND
GERMANY
EUROPE
FRANCE
SPAIN
Odessa
Black Sea
TURKEY
GREECE
Azores
Madeira
Canary Is
Rabat
Marocco
Saffi
Mogador
Algeria
Cilicia
Syria
Egypt
0°
<0°
4°
5°
6°
7°
8°
9°
10°
13°
13,9
DISTRIBUTION OF FRESH-WATER EELS.
(ANGUILLA)
Atlantic fresh-water eels (Ang. vulgaris & chrysypa) present.
Indian fresh-water eels present.
Fresh-water eels absent.
7° —— to show the temperature in 1000 meters depth.
● to show the places where larvae of Atlantic fresh-water eels were found by the author and by American observers.

sity will therefore cause the mean age in the catch to vary, but it affects the number of eels caught only marginally. Lower fishing intensity tends to increase the size at catch but hardly affects the number of eels caught. Therefore, commercial yield provides some index of stock size.

This study seeks to quantify the spatial variation in density of the eel stock. In combination with estimates of the amount of habitat available, this completes the zoogeography of the eel. Finally, the life stage targeted by the fishery will be related to the stock abundance and density.

Material and methods

Data

Data on commercial yields were collected from the literature, starting from three previous reviews of available data (Aubrun 1986, 1987; Moriarty 1997; Moriarty and Dekker 1997). Additionally, the literature listed in Tesch (1999) and in ASFA-1 (FAO 1998) was examined. Data sources were included whenever the following information was specified.

(*a*) Commercial yield in weight and whether it concerns either glass eel or yellow/silver eel. (Fisheries on wild eel, as well as fisheries on stocked eel, were included. Also, semi-commercial fisheries for glass eel for restocking purposes in northern countries were included.)

(*b*) Reference year (in line with Moriarty and Dekker (1997), data for 1993 were preferred, or a year close to that).

(*c*) Water body or river system. For (large) river systems, the location of the river mouth was used in the analysis. For lakes, lagoons, and reservoirs, a position near the centre was used. Longitude and latitude were rounded to

Table 1. Literature sources on commercial yield of eel and the type of surface area measure used.

	Glass eel fisheries		Yellow/silver eel fisheries	
	Number of records	Accumulated catch (t)	Number of records	Accumulated catch (t)
Data sources				
Aker and Koops 1974	0	0	1	300
Anwand and Valentin 1981*a*, 1981*b*	0	0	4	29
Aubrun 1986, 1987	19	264	9	394
Dekker 2002*b*	5	2	0	0
Elster and Jensen 1960	0	0	1	1
FAO 2000	0	0	1	3
Gagneur and Kara 2001	0	0	1	32
Hahlbeck 1992	0	0	7	34
Kangur 1998	0	0	1	85
Moriarty 1991	0	0	1	50
Moriarty 1997	29	388	67	8 027
Müller 1961	0	0	10	429
Navaz y Sanz 1964	1	275	0	0
Paetsch 1983	0	0	2	59
Paulovits and Biro 1986	0	0	1	115
Pedersen 1997	0	0	3	111
Tesch 1967	0	0	6	25
Vallet 1977	0	0	1	<1
Wickström and Hamrin 1997	0	0	11	64
Zaouali 1977	0	0	1	97
Unpublished	0	0	7	1 160
Sum	54	929	134	11 002
Surface area measure				
Water surface area	5	5.5	123	10 380
Drainage area	49	924	11	622

Note: "Accumulated catch" might double-count individual fisheries when published in two sources; also, some publications list both surface area measures.

one minute. Data by country (Fig. 2) do not refer to natural geographical entities and were only used in the analysis of the life stage targeted by fisheries.

(*d*) Surface area of either the water body (wet surface) or the drainage area of the catchment (wet and dry surface combined). If not given, the surface area was derived from any other source available (including searches on the Internet) or was roughly estimated from the *Times Atlas of the World* (Times Books 2001). For countries, land and water surface areas were derived from CIA (2001).

In total, 199 data records were identified, with a cumulative yield of 11 932 t of eel (Table 1; Fig. 2).

Surface area measure and exploited life stage

Literature sources list surface area of drainage systems or surface area of a water body. The relation between the two measures is far from clear. The water surface area of a river system depends not only on the precipitation and evaporation rates, the type of soil, the slope, etc., but also on the magnitude of the system, larger rivers having relatively more water surface. Moreover, for rivers representing fractals (Tarboton et al. 1988), water surface is not easily measured. Consequently, there is no universal way to convert drainage system areas into equivalent water surface areas.

Commercial fisheries in some areas target for glass eel, but elsewhere, yellow/silver eel prevail (Dekker 2000*b*). The glass eel fisheries are negligible in terms of weight but take by far higher numbers (Moriarty 1997). The relation between the number of glass eel entering a river and the corresponding number of (market size) yellow eel available to the fisheries depends on the natural mortality rate and the duration of the stage between. Hence, there is no obvious way of comparing yields from glass eel fisheries with those from yellow/silver eel fisheries.

By cross-tabulating the surface area measure used and the life stage being fished (Table 1), the complexity of the problem appears to be manageable: glass eel fisheries operate in river mouths, for which the drainage area is known, whereas fisheries for yellow/silver eel are largely restricted to lakes and lagoons, for which the water surface is known. A minor quantity of yellow/silver eel data (5%) stems from running waters.

Absence of eel

Few studies report the absence of eel. Schmidt (1909) explicitly reports on absence or presence of eels. Absence (23 records) was interpreted as a zero yield, for both glass eel and yellow/silver eel, in lakes as well as in rivers. Secondly, some sources (Table 1) report on one life stage, implicitly or explicitly excluding other life stages (15 records for glass eel, one for yellow/silver eel). Thirdly, Schmidt (1909) argued that *A. anguilla* (L.) does not occur outside the outer limits of the distribution in Europe and northern Africa. These

Fig. 2. Raw data on yield of eel fisheries per country (background) and per water system (symbols). Yield per surface area is expressed by the gray scale of the areas. For individual water systems, the size of the plotted symbols is proportional to the root of the surface area, but water surface areas have not been drawn in proportion to drainage areas. (*a*) Glass eel yield (kg·km^{-2} drainage area) in rivers and per country. (*b*) Yellow/silver eel yield (kg·km^{-2} water surface) in lakes–lagoons and per country. Legend for Figs. 2*a* and 2*b*: units in kg·km^{-2}; the scale is logarithmic equidistant.

implicit zero observations surrounding the distribution in Europe–Africa were implemented as a series of explicit zero records at 10° intervals, along the frame 25–75°N, 20°W–40°E, for both life stages and in lakes as well as in rivers (22 records). Finally, Aubrun (1986, 1987) covers all drainage systems along the French coast, including the systems without glass eel fisheries (eight records). Overall, the number of zero records totals 68 for glass eel and 46 for yellow/silver eel.

Analysis of distribution

The logarithm of the yield per surface area (glass eel, drainage system area; yellow/silver eel, lake or lagoon surface area) was analysed using a geostatistical model (Cressie 1993). No fixed effects were included. The spatial component included a Gaussian covariance structure (range and sill) and a nugget effect. Euclidean distances between observations were calculated in degrees, treating degrees longitude and latitude alike. One degree latitude spans 111 km, whereas one degree longitude spans 101 km at 25°N, 72 km at 50°N, and only 29 km at 75°N.

Logarithms of zeroes were avoided by adding a small quantity, equal to the lowest (positive) observation, to all observations: 1.35 g·km^{-2} (drainage area) for glass eel and 2.7 kg·km^{-2} (water surface area) for yellow/silver eel.

The model was implemented in SAS (SAS Inc. 1999). The spatial distribution was reconstructed by ordinary kriging (random effects), using "proc krige2d" with parameters estimated by "proc mixed".

Analysis of life stage in fisheries

To analyse the relation between stock density and the life stage targeted by the fishery, data were selected quantifying the yield per life stage. For glass eel, yield density was expressed per drainage area. Comparison of glass eel catch to yellow/silver eel catch therefore restricted the data set to records listing catch of yellow/silver eel per drainage area, i.e., countries and some rivers. Following Dekker (2000*b*), the French data were partitioned between the Atlantic and the Mediterranean coasts and the British data among the Severn area, Northern Ireland, and the rest of the U.K. For several countries, a small yield of glass eel used for restocking was not recorded as commercial catch by Moriarty (1997); using data from Dekker (2002*b*), these restocking catches were added. For the comparison of yellow to silver eel yield, only the records specifying these life stages separately can be used.

The number by life stage in the catch was calculated assuming 3000 glass eels and 5 yellow or silver eels per kg (Moriarty 1997). The fraction of one life stage in the total yield was arcsine transformed ($y = \arcsin \sqrt{\text{fraction}}$) and plotted versus the logarithm of yield density (number·km^{-2}). A regression line was fitted to the transformed data, including observations with a zero yield in one of the life stages. Because the plotted axes were both based on the same observed quantities, they were not independent and no formal statistical tests were applied.

Results

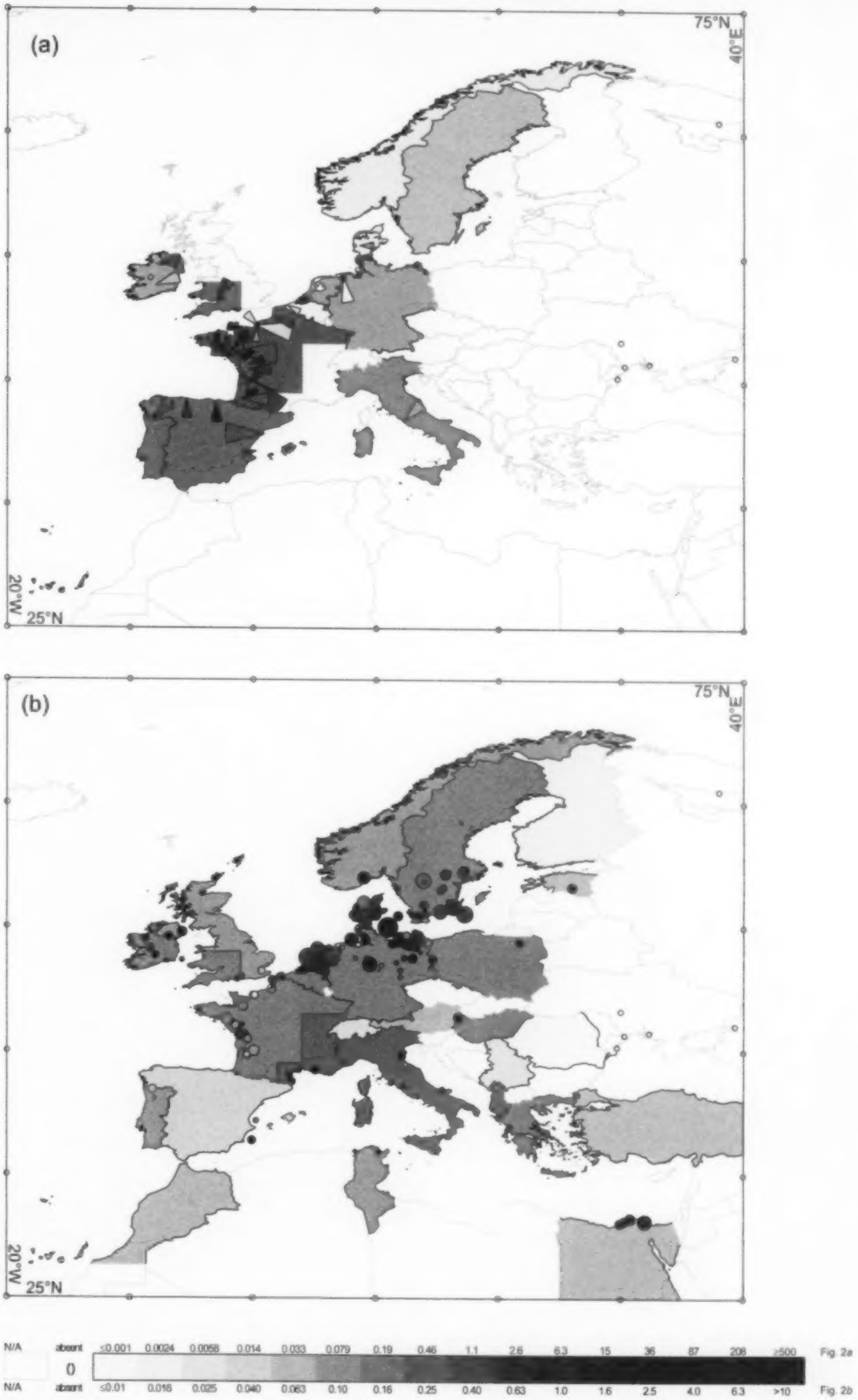
For glass eel fisheries, data were obtained from France, the Iberian Peninsula, the British Isles, and several more isolated locations (Fig. 2*a*). Yields ranged from 1.35 (River Ems, Germany) and 6.25 g (River Risle, France) to 75 (Cap Breton, France) and 500 kg (Isle de Ré, France) per km^2 of drainage area.

For yellow/silver eel fisheries, data were obtained from all over Europe and northern Africa, with the highest concentration of data in the Netherlands, Germany, Denmark, and Sweden (Fig. 2*b*). Yields ranged from 3 kg (Golf du Morbihan, France, and several hafs in eastern Germany) to 8 (Vie, France) and 32.4 t (Monaci, Italy) per km^2 of water surface.

The area over which data on the glass eel fisheries were available is much smaller than for the yellow/silver eel fisheries. Consequently, the variogram for the former (Fig. 3*a*) spanned a smaller range of distances than for the latter (Fig. 3*b*). In both data sets, the variation between mutually remote observations was only marginally higher than between nearby observations: for the glass eel fisheries, nearby observations varied by a factor of 10 on average, and remote observation pairs (20° apart) by a factor of 20, whereas for the yellow/silver eel fisheries, these factors are 4 and 10, respectively. For the yellow/silver eel fisheries, maximum differences (up to a factor 10 000) occurred at distances of 10–20°, whereas at greater distances (30–40°), only smaller ratios in yield density (<100–<10) were found. The range of the fitted variogram was 8.1° (latitude or longitude) for the glass eel and 12.5° for the yellow/silver eel data.

Using these estimates, kriging of the primary data (Fig. 4) showed highest yield in glass eel fisheries to occur in the southeastern corner of the Bay of Biscay and on the eastern Mediterranean coast of Spain. Some isolated high spots were found in central Brittany and just south of Brittany (Isle de Ré, France). The area of highest abundance ended gradually in the Iberian Peninsula, owing to the absence of data. The Iberian glass eel fishery is not well documented; therefore, this analysis may wrongly suggest a southern limit to the distribution of glass eel fisheries. For the yellow/silver eel fisheries, the distribution was much wider, with highest yields around the western Mediterranean. Isolated high and low spots occurred, most notably in eastern Germany, where relatively high and low observations were found close together.

The life stage targeted by fisheries (Fig. 5) showed a clear relationship with density of the eel stock. Glass eel fisheries were absent at yield densities of 0.04–50 eels·km^{-2} (drainage area) and occurred at 15–2300 eels·km^{-2}. With increasing yield, the fraction in the catch (by number) increased from a few percent (in countries with glass eel fisheries for restock-


(a)
75°N
40°E
20°W
25°N
(b)
75°N
40°E
20°W
25°N
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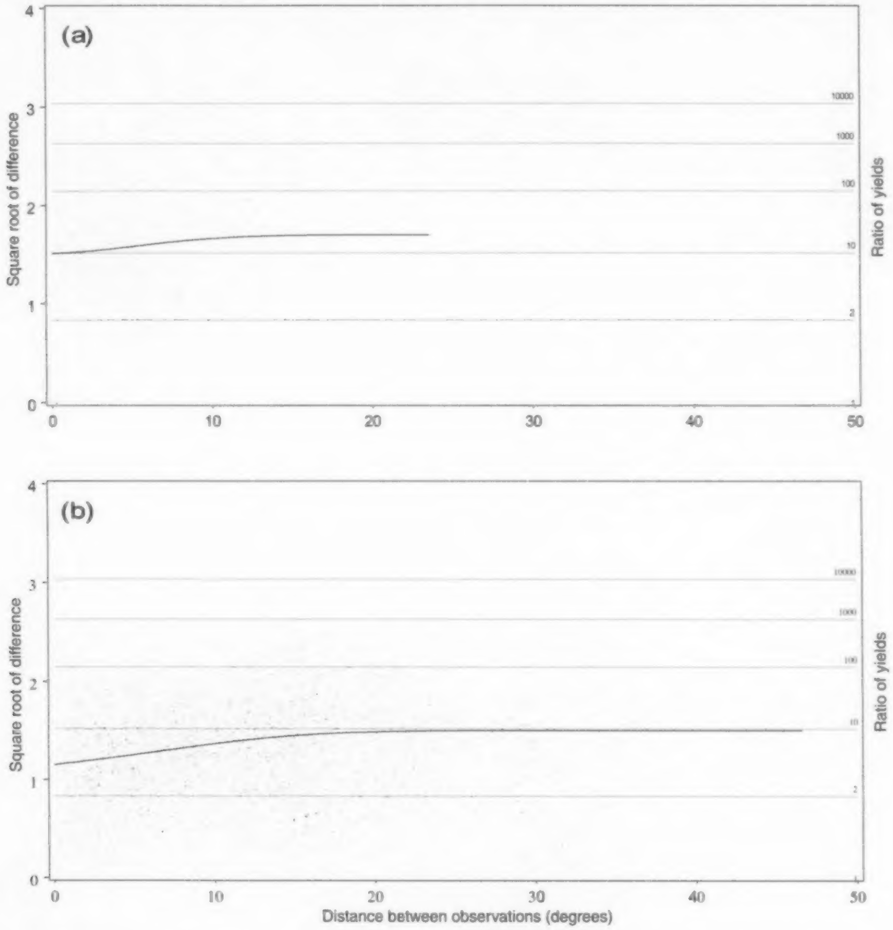
absent
0
≤0.001 0.0024 0.0058 0.014 0.033 0.079 0.19 0.46 1.1 2.6 6.3 15 36 87 208 ≥500
Fig. 2a
N/A
absent
≤0.01 0.016 0.025 0.040 0.063 0.10 0.16 0.25 0.40 0.63 1.0 1.6 2.5 4.0 6.3 >10
Fig. 2b

Fig. 3. Variogram of the yield of eel fisheries per unit surface area. The left axes refer to the log-transformed data, the right axes to the corresponding untransformed observations. Points represent observations; line represents fitted Gaussian variogram. Zero observations have been left out. (*a*) Glass eel fisheries, yield per drainage system area. (*b*) Yellow/silver eel fisheries, yield per water surface area.



ing) to nearly 100% in the U.K. (Severn area), France (Atlantic), Spain, and Portugal. Silver eel catches were inversely related to yield density in lakes (Fig. 5*b*) and were not reported at all in coastal areas. At a density of 1000 eels·km^{-2} water surface, silver eel made up around 50% of the catch in lakes, declining to almost nil at 50 000 eels·km^{-2}.

Discussion

Distribution area

According to Schmidt (1909), the European eel is distributed "from North Cape in Northern Norway and southwards along the coast of Europe, on all the coasts of the Mediterranean … and on the north-western part of the coast of Africa". Although this statement may be correct in a qualitative sense, it ignores the quantitative distribution of the stock within the area and as such is an oversimplification. Schmidt used a gradually thinning line to depict a declining density in the northern reaches of the Baltic and in the Propontis (Sea of Marmara), but elsewhere, all coasts were marked by a line of constant width. However, major concentrations of glass eel recruiting from the ocean did and do appear in France and Spain, whereas highest productivity of coastal and inland waters occurs in areas bordering the western Mediterranean. Re-analysis (Fig. 6) of the information presented in texts by Schmidt (1906, 1909) reveals the concentration of recruitment in the Bay of Biscay. These areas were listed by Schmidt under the heading "Elvers as food" and in his context, "elvers" only indicated glass eel. However, his detailed data records were limited to areas north of 43°N, and although this limitation was re-iterated in the text, it is ignored completely in the final distribution map.

Use of fishing yield data

The analysis presented in this article is based on data derived from commercial fisheries, rather than on experimentally assessed data of stock density, as the latter show great spatial and stochastic variation. However, this choice might have biased the analysis, especially for the glass eel fisheries. Observations are largely restricted to a small area with high yield. High yields will be a prerequisite for commercial exploitation. However, noting the (positive) relation between yield density and the fraction of glass eel in the yield, absence of data on commercial exploitation outside the typical "glass eel exploitation area" may well be the consequence of low stock densities. In addition, the data on glass eel fisheries for restocking do fit in well.

Shortage of data

The high variability of experimental stock surveys (Barak and Mason 1992; Knights et al. 1996) is also manifested in the commercial yield data in that the broad-scale variation is hardly larger than local variation (nugget effect). Where information is lacking (e.g., for large parts of the Iberian Peninsula), a smooth cline is fitted towards the trivial absence records at the outer limit of the study area. However, such a smooth cline would not adequately describe the local patterns in data-deficient areas. To fill this gap, information on glass eel fisheries in the Iberian Peninsula and northwestern Africa and yellow/silver eel fisheries in the Balkan, the eastern Mediterranean, and northern Africa is required, as it has been since Schmidt (1906).

Density and abundance

The analysis of glass eel abundance was based on the yield·km^{-2} of drainage area. For most of the distribution, this results in an estimate of the absolute yield. In northern Africa, large areas do not have any surface water drainage but are expected to have negligible recruitment. In the Iberian Peninsula, where semi-arid conditions prevail, recruitment is concentrated in few, relatively small streams draining a large area. Such concentrations in smaller rivers should facilitate exploitation and might explain the occurrence of glass eel fisheries down to the southern range of the distribution area (Portugal, Morocco) and their comparatively high share in the yield.

For yellow/silver eel, yield was calculated in relation to water surface area. The estimated density does not correspond to absolute yield, because habitat availability varies greatly from region to region. Quantitative data on habitat availability can be acquired from climatological databases, but these only cover fresh water. Global climatological databases (e.g., Cogley 1994) combine lagoons, estuaries, open ocean, and exposed rocky shores into a single category (saline waters), including habitats that are well suited and unfit for eel. Although this does not allow a detailed analysis, some general trends can be inferred (Fig. 7). From north to south, permanent lakes peak at about 60°N (Scandinavia), whereas the number of permanent rivers remains high and rather constant down to 35°N (African north coast). Farther south, rivers as well as lakes dry up completely, which makes it unlikely that any freshwater habitat is permanently available. Consequently, although yield per surface area in the western Mediterranean is high, production in fresh water will be low, total production being dominated by marine catches. For Tunisia, for instance, statistics (FAO 2000) list 55 t·year^{-1} (averaged over the 1990s) from inland waters and 244 t·year^{-1} from marine waters. It is noteworthy that scarcity of fresh waters in northern Africa is a relatively recent phenomenon. Reale and Dirmeyer (2000) provided substantial evidence of higher precipitation, more abundant fresh water, and richer vegetation during the Roman Classical Period. Anthropogenic degradation of the vegetation might have changed the climate irreversibly to the current desert conditions (Reale and Shukla 2000). Hence, one may wonder whether eel has been as abundant in Roman Africa as in Roman Italy, where many remains of eel culture have been found (Higginbotham 1997).

Northern limit

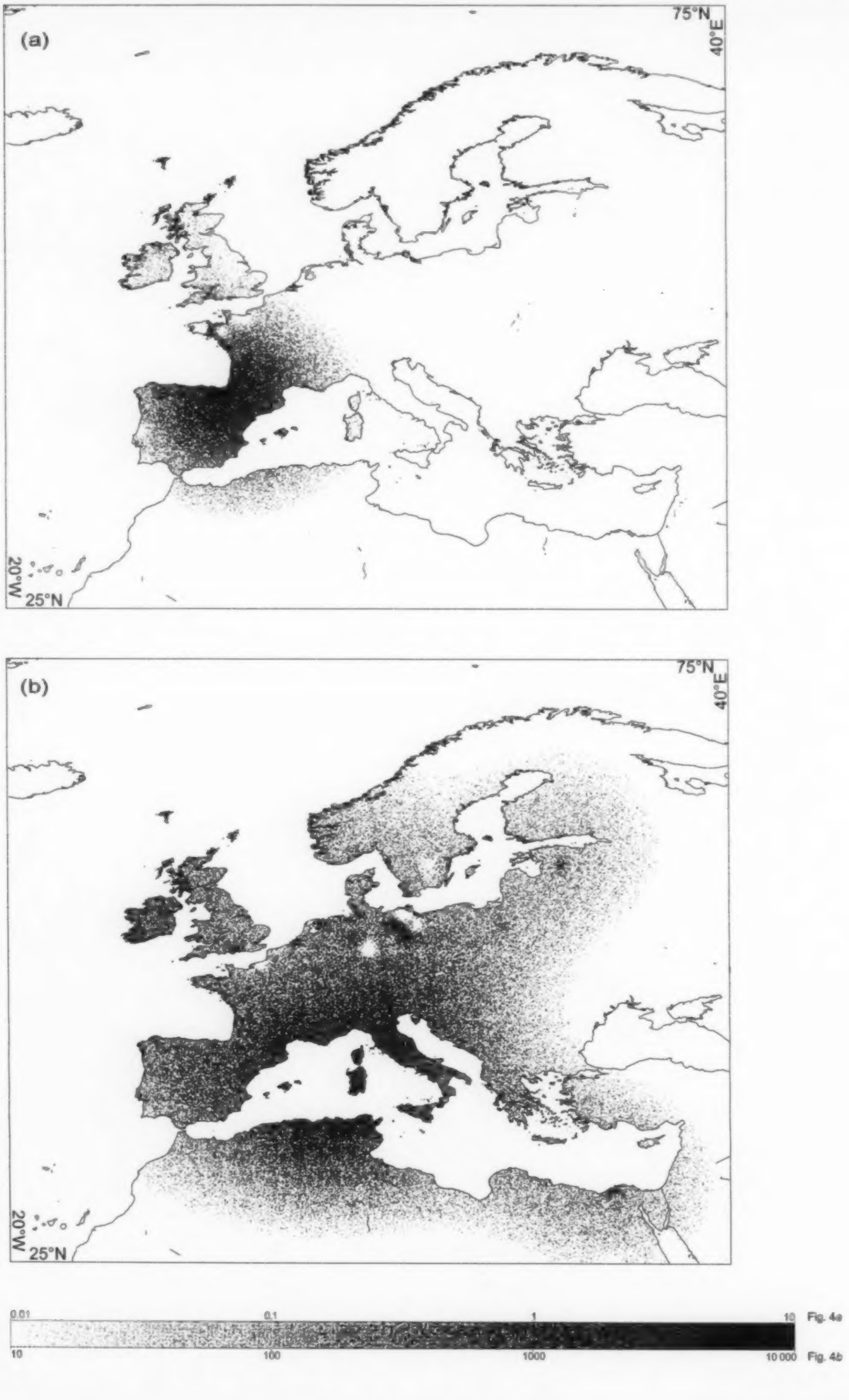
To the north, Schmidt (1909) took the North Cape as the effective limit of the distribution. The exact location has attracted some discussion (Ege 1939; Sorokin and Konstantinov 1960). The gradual decline towards the north, through Norway, conforms to the Norwegian catches presented by Schmidt (1909): 267 t for areas south of Trondheim (63°N) and only 230 kg for the lengthy coast (>1000 km) farther north. Apparently, the distribution area has no sharp northern limit but gradually fades out. The stock in Iceland has recently attracted attention because of its peculiar genetic make-up, a sympatric occurrence of the European eel and the American eel (*Anguilla rostrata*) and interbreeding of these two species (Avise et al. 1990). However, Iceland has never reported any commercial eel catches. Iceland appears to be at the outer fringe of the distribution.

Southern limit

"In order to understand the distribution of the eels, especially that … they have not been able to penetrate further southwards on the coasts of the Atlantic …", Schmidt (1909) discusses the conditions at the spawning location (i.e., deep and warm water, "more than 7°C at a depth of 1000 meters"). In his view, the conditions "of the adjacent seas" off the African west coast, from about the Tropic of Cancer southwards, are unsuitable for reproduction. Remarkably, the condition of adjacent warm and deep water does not hold for nearly the entire distribution area. In addition, this requirement does not match with his view on the "spawning places" in the Sargasso Sea, at a distance of more than 3000 km from West Africa. His inference was based entirely on the presence or absence of eels in continental waters, as deduced from correspondence with Danish Consuls and available literature. Considering the results obtained now and noting the climate conditions in Africa, I propose that absence of continental habitat is a more likely cause. Over a distance of more than 1000 km, there is hardly any suitable habitat. Indeed, where fresh waters are locally abundant (e.g., rivers on the Canaries), a substantial eel stock can be found (H. Encarnaçao, Funchal, Madeira, Portugal, personal communication) and recruitment does not appear to be a bottleneck. That raises the question of whether a fringe of declining numbers of recruits can be found in the ocean farther south. Because the number of observations in this area is low (Boëtius and Harding 1985), this question cannot be answered at present.

Distribution of fisheries

The distribution of fisheries is generally described as glass eel fishing being concentrated in southern areas and silver eel fishing dominating in the north (Moriarty and Dekker 1997). Current results suggest that stock density controls what life stage can be targeted. Glass eel fisheries are found


(a)
75°N
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(b)
75°N
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20°W
25°N
0.01
0.1
1
10
Fig. 4a
10
100
1000
10 000
Fig. 4b

Fig. 4. Kriging eel fishing yield per surface area. Spatially predicted values are scaled between minimum and maximum observed values, represented by dithered gray scales: the higher the density of pixels, the higher the yield. Note the logarithmic transformation of the yield. (*a*) Yield of glass eel per river drainage area. (*b*) Yield of yellow/silver eel per water surface area. Legend for Figs. 4*a* and 4*b*: units in kg·km^{-2}; the scale is logarithmic.

Fig. 5. Relationship between the density of the eel harvest and the life stage being exploited. The horizontal axes are on logarithmic scale; the vertical axes list the fraction that a given life stage constitutes of the total catch as a percentage, but values have been arcsine-transformed. (*a*) Percentage glass eel in the total yield. Individual points represent different countries; non-zero observations have been labelled with a country code. (*b*) Percentage silver eel in the yield of yellow and (or) silver eel. Individual points represent different water bodies; solid symbols for fresh waters, open symbols for coastal areas.

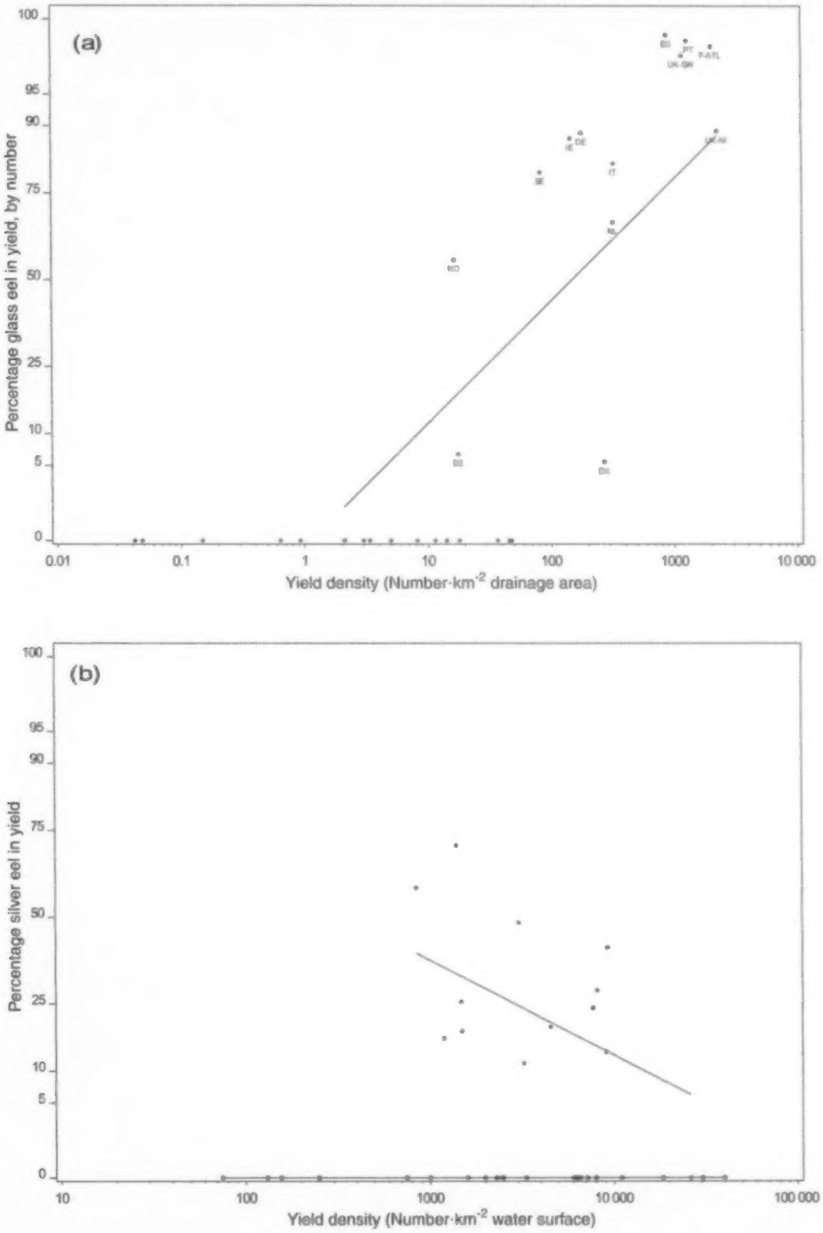
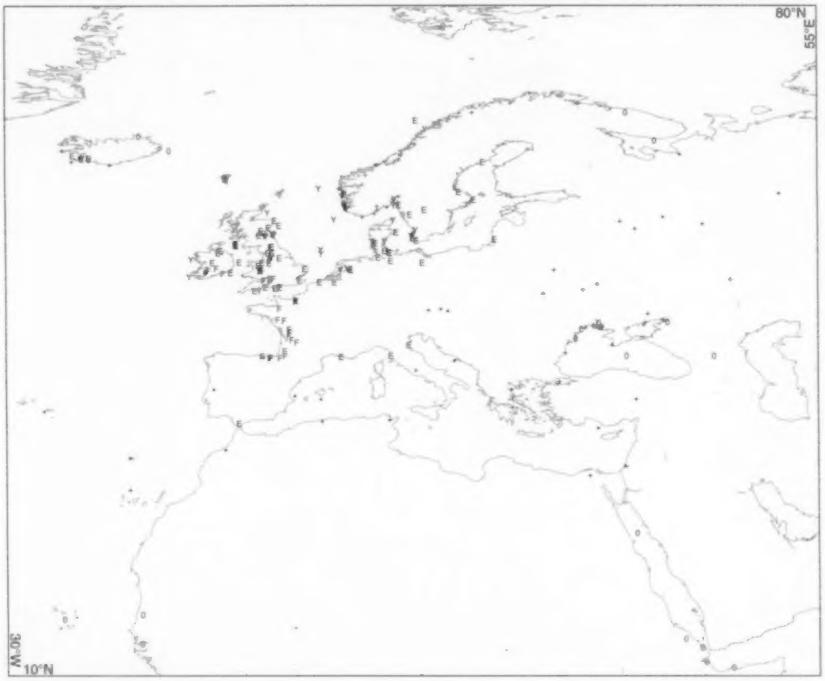


Fig. 6. Distribution data provided by Schmidt (1906, 1909, 1925) in the text of his publications. Schmidt lists many place names and rivers, which have been located and displayed in this map. Symbols indicate the descriptions given by Schmidt; his context indicates that he used "elvers" only for glass eel. Legend: 0, absent; +, present; F, elvers as food; Y, young eels in the sea; E, elvers into fresh water.



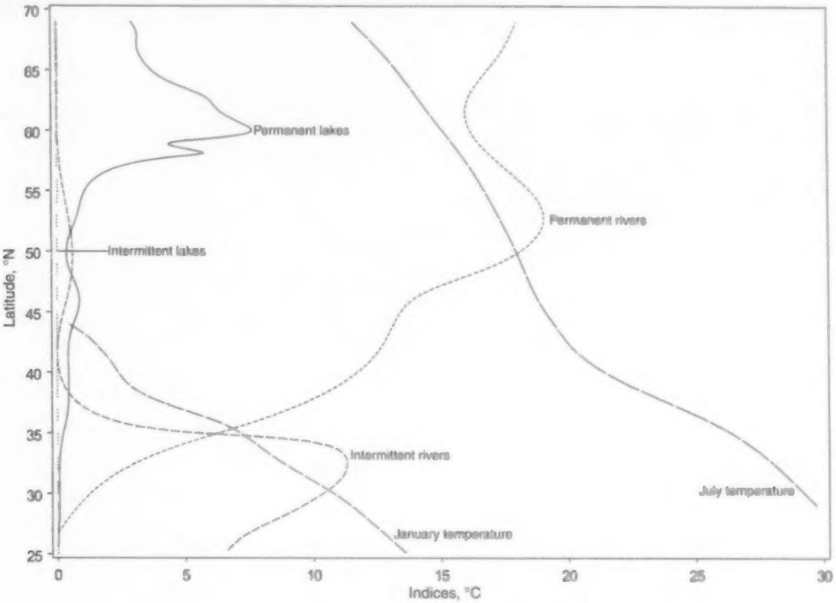
in the centre of the distribution, where stock density is at a maximum, and in more southerly regions, where the incoming recruitment is concentrated in less and smaller rivers. The predominance of silver eel in northern areas has been interpreted as northern areas producing the major portion of the spawner escapement (Castonguay et al. (1994) for the American eel; Svärdson (1976) for the European eel); however, silver eel yield in northern, sparsely populated areas is actually lower than closer to the centre. At a yield of 1000 eels·km^{-2} of water surface, 370 eels will be silver (37%), whereas at 10 000 eels·km^{-2}, the yield comprises 1300 silver eels (13%). This suggests that the dominance of silver eel in northern catches is probably better understood as an adaptation of the fisheries to low stock densities, that is, as a consequence of the truly low silver eel abundance. Silver eel fisheries attain the maximal yield per recruit (Vøllestad 1990), and the concentration in time (autumn) and space (lake outlets and river mouths) of the silver eel run increases the efficacy of the fisheries. The focus of the northern fisheries on silver eel thus may reflect a retreat from nonprofitable yellow eel fisheries.

Cultural patterns in fishing and consumption have been mentioned as factors determining the distribution of fisheries (Moriarty and Dekker 1997), especially for glass eel exploitation, interfering with the relation between stock density and fishing yield. However, comparison of Schmidt's information on glass eel consumption in the early 1900s (Fig. 6, "Elvers as food") with present-day information (Moriarty and Dekker 1997) shows that the tradition of glass eel consumption is lost in England, Wales, and Ireland in the course of the 20th century. French glass eel was used for local consumption in the early 1900s but is now mainly exported to Spain and Eastern Asia (Dekker 2002*a*). Legal constraints in southern countries (e.g., Spain, Portugal; Moriarty and Dekker 1997) hardly preclude actual fishing. In northern countries, glass eel fisheries for restocking replace commercial exploitation. Clearly, so-called traditional fisheries adapt easily to stock abundance and market options, whereas legislation modifies rather than determines exploitation.

Biogeography

Most *Anguilla* species inhabit tropical waters (Schmidt 1925; Tsukamoto and Aoyama 1998). Large-scale commercial exploitation, however, is largely confined to temperate waters (Dekker 2002*a*). The temperate species (*A. anguilla*, *A. rostrata*, *A. japonica*, *A. australis*, and *A. dieffenbachia*) are described to "have left the tropical zone to spread out beyond the tropics and as far as the polar circle" (Bertin 1956; "polar circle" applies only to the European eel). The high yield of the European eel in temperate areas is in strong contrast with the temperature preference of the species, ranging from 10 (Boëtius and Boëtius 1967) to 38°C, with an optimum of 22–23°C (Sadler 1979). The optimum temperature, routinely applied in aquaculture (Kamstra 1999), only occurs in the southern part (south of 40°N) of the distribution area (Fig. 7). Since Schmidt (1909), the absence of eel (of any species) in the southern Atlantic has attracted considerable debate, but discussion has focused on oceanographic condi-

Fig. 7. Distribution of freshwater habitats and summer and winter temperature by latitude, averaged over the study area. Note that the axes have been interchanged to plot (northern) latitude in the vertical.



tions exclusively (Schmidt 1925; Bertin 1956; Tsukamoto and Aoyama 1998). The southern limit of the distribution is more likely to be determined by the absence of continental habitat in the Sahara. Penczak and Molinski (1984) describe the most extreme case: a river 150 m wide, completely drying up in summer, with only one small pool left; afternoon water temperature approaching 40°C in which they catch an eel alive. An arid zone has been found in northwestern Africa throughout the period of speciation of the Atlantic eels (Kutzbach and Ziegler 1993) and therefore may have been of evolutionary significance for the European eel. On the American side of the Atlantic, no desert zone exists and the American eel is indeed found much farther south, down to Guyana, about 5°N (Schmidt 1909), and glass eel has been exploited as far south as 21°N (Fernandez and Vazquez 1978). For the other species, only a smaller desert zone occurs in the northwestern Indian Ocean, but the distribution of the species involved, *A. bicolor* and *A. marmorata*, extends on both sides of that zone (Schmidt 1925).

A major portion of the yield of the European eel is produced in the Mediterranean (Table 2) at temperatures in accordance with the species' and genus' preference. However, production in more northern areas, at ambient temperatures far below optimum, is also substantial. Apparently, the distribution area extends beyond the area of optimum conditions. In comparison with other eel species, larval migration from the suspected spawning grounds in the Sargasso Sea to the eastern shores of the Atlantic covers an extremely large distance, over 3000–7000 km (Schmidt 1925). Noting that transport of larvae to the continent is possibly only through passive drifting (McCleave et al. 1998), the northern areas presumably receive only the accidental diaspora of larvae, straying from their long route to more favourable continental areas. If so, recovery of the stock (ICES 2001) crucially depends on the southern European and northern African countries, which so far have only marginally been involved in scientific- and management-related initiatives to address the poor state of the stock (Moriarty and Dekker 1997; ICES 2002).

Table 2. Statistics on landings of river eel (FAO 2000), averaged over the 1990s, with minor corrections (W. Dekker, unpublished data), broken down by major drainage basin and fishing area.

Drainage	Inland fisheries	Coastal fisheries	Grand total
Atlantic Ocean	4923	4089	9 012
Mediterranean	4520*	1524	6 043
Inland countries	493	0	493
Grand total	9936	5613	15 549

Note: Countries not bordering the sea have been included under a separate heading, Inland countries, regardless of their drainage.

*Includes ~2300 t of eel from extensive outdoor aquaculture in Italy, mostly using Italian glass eel.

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Difficulties in relating Cd concentrations in the predatory insect *Chaoborus* to those of its prey in nature

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Abstract: Because *Chaoborus* larvae take up most of their cadmium (Cd) from food, we tested the hypothesis that Cd concentrations in this insect are directly related to those in their planktonic prey. We measured Cd in *Chaoborus* and in zooplankton collected from 24 eastern Canadian lakes varying widely in their Cd concentrations. Cd concentrations in the predator were not correlated with those in bulk zooplankton, whether separated into size fractions liable to be eaten by *Chaoborus* or not. In highly acidic lakes, Cd concentrations in *Chaoborus* did not respond to increases in zooplankton Cd because of either competition between H and Cd ions at Cd absorption sites in the predator's gut or differences in prey community composition between highly acidic and circumneutral lakes. Relationships between Cd in *Chaoborus* and in its potential prey were stronger when we used Cd concentrations for specific crustacean taxa in a mechanistic model. We conclude that predictive relationships between metal concentrations in predators and their prey are likely to be strongest if the subset of prey consumed by the predator has been characterized and if this information is used in a bioaccumulation model.

Résumé : Parce que les larves de *Chaoborus* tirent la plus grande partie de leur cadmium (Cd) de leur nourriture, nous avons vérifié l'hypothèse selon laquelle les concentrations de Cd chez cet insecte sont directement reliées à celles de leurs proies planctoniques. Nous avons mesuré les teneurs en Cd de *Chaoborus* et du zooplancton dans 24 lacs de l'est du Canada dont les concentrations en Cd variaient considérablement. Les concentrations de Cd chez ce prédateur n'étaient pas reliées à celles du zooplancton global, qu'il soit séparé ou non en fractions de taille susceptibles d'être consommées par *Chaoborus*. Dans les lacs très acides, les concentrations de Cd chez *Chaoborus* ne reflétaient pas les concentrations de Cd du zooplancton, soit en raison d'une compétition entre les ions H^+ et Cd^{2+} aux sites d'absorption du Cd dans le tube digestif du prédateur, ou alors en raison de différences dans la composition des communautés de proies entre les lacs très acides et les lacs proches de la neutralité. Les relations entre les teneurs en Cd chez *Chaoborus* et celles de ses proies potentielles se sont avérées plus significatives lorsque les concentrations de Cd de taxons particuliers de crustacés furent utilisées dans un modèle mécanistique. En conclusion, le pouvoir prédictif des relations entre les concentrations de métaux chez les prédateurs et leurs proies sera vraisemblablement accru si les proies véritablement consommées par le prédateur ont été bien identifiées et si ces renseignements sont utilisés dans un modèle de bioaccumulation.

[Traduit par la Rédaction]

Introduction

Industrial activities have increased the entry of trace metals into aquatic environments (Pacyna et al. 1995). To improve our ability to predict the biological impact of these pollutants and to conduct meaningful ecological risk assessments for aquatic communities, we need to better understand the accumulation of metals by organisms (Pace 2001). In aquatic systems, metals are accumulated by primary producers (St.-Cyr and Campbell 1994; Luoma et al. 1998) and then transferred to animals at higher trophic levels (Fisher and Reinfelder 1995). The diet, as opposed to water, is an important route of metal accumulation for many animals (Schlekat et al. 2001). As a consequence, risk assessments that do not consider dietary metal exposure can underestimate animal metal concentrations and resulting effects on target species in nature (Chapman and Wang 2000). A consequence of dietary metal uptake is that metal concentrations show trends along food chains. Thus concentrations of lipophilic forms of mercury and selenium are reported to increase with increasing trophic level (Luoma et al. 1992; Cabana et al. 1994; Chen et al. 2000), whereas the results of several laboratory studies suggest that the concentrations of nonlipophilic metal forms tend to decrease along freshwater

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food chains (Hatakeyama and Yasuno 1987; van Hattum et al. 1989; Croteau et al. 2001). In the field, trends in trace metal concentrations along planktonic food chains are difficult to discern because feeding relationships between organisms at various trophic levels are usually not known (Hare 1992) and because of the difficulty in obtaining sufficient biomass for measuring metals in small-sized organisms such as copepods and cladocerans. Because of this latter limitation, most investigators measure metals in bulk plankton samples (Chen and Folt 2000; Chen et al. 2000). However, bulk plankton includes a wide range of animal types, sizes, and trophic levels that could obscure trends in metal concentrations along food chains (Watras and Bloom 1992).

We set out to determine if cadmium (Cd) concentrations in the predator *Chaoborus* are related to those in zooplankton, the major source of Cd for this insect (Munger and Hare 1997; Munger et al. 1999). No previous field studies have attempted to relate Cd concentrations in a planktonic predator to those in its prey. We collected zooplankton and final instar *Chaoborus* larvae from a large number of lakes located along a Cd gradient in eastern Canada. Then we compared Cd concentrations in *Chaoborus* with those measured in either bulk zooplankton or in zooplankton subfractions separated according to size (*Chaoborus* is a gape-limited predator; Hare and Carter 1987) or taxonomic group (cladocerans and copepods). Lastly, we incorporated these measurements into a mechanistic Cd bioaccumulation model (Croteau et al. 2001, 2002) to determine if this laboratory-based model could successfully predict Cd concentrations in the predator from those measured in these various fractions of zooplankton.

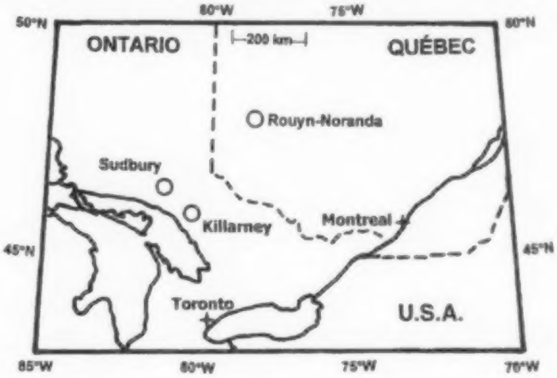
Methods

Collection of field samples

We collected samples of invertebrates and water between 1996 and 1998 from a series of lakes located on the Canadian Shield in the mining areas of Sudbury (Ontario) and Rouyn-Noranda (Québec) (Fig. 1, Table 1). Samples were collected only in the spring (late May to mid-June) to minimize confounding seasonal changes in *Chaoborus* Cd concentrations among sites (Hare and Campbell 1992).

Chaoborus larvae were collected after sunset near lake centre by hauling a 250 μm mesh aperture plankton net horizontally in the water column of each lake (Table 2). We transported live animals to the laboratory in plastic bags filled with lake water. *Chaoborus* larvae were identified to species using the keys in Saether (1972), and final (fourth) instar larvae were selected on the basis of head capsule lengths as given in Larow and Marzolf (1970; *C. punctipennis*), Fedorenko and Swift (1972; *C. americanus*), and Parma (1971; *C. flavicans*). We chose final instars because they were the predominant instar in most spring samples, because they provide a larger mass for Cd analyses than do younger instars, and because they consume the greatest range of prey types and sizes (Hare and Carter 1987; Moore 1988). We held larvae in their original lake water for 12–24 h to eliminate their gut contents. Where numbers permitted, we placed five replicate samples of 3–15 *Chaoborus* larvae (or 1 larva per sample from Lake Hélène) on pieces of preweighed acid-washed Teflon sheeting that were frozen until Cd analysis. Although we treated larvae whole, trends in larval Cd would not have differed if we had measured Cd in only the major organ of accumulation, that is, the gut, because almost all larval Cd (~95%) is found in this organ (Croteau et al. 2001). As a corollary, because little Cd is associated with the larval exoskeleton (<5%), differences among larvae in the time since their last moult should have no influence on their Cd concentrations.

Fig. 1. Locations of our three study areas (Rouyn-Noranda, Sudbury, and Killarney) in eastern Canada.



We collected other planktonic organisms just before sunset by horizontally hauling a 64 μm mesh net near the centre of each lake; the net's path ensured that plankton was collected from all depths. Aliquots of this plankton were placed in plastic bags with lake water. Remaining bulk plankton was gently poured over a series of acid-washed nylon sieves of four mesh sizes (1000, 500, 300, and 64 μm); animals (mainly *Holopedium gibberum*) and debris retained by the 1000-μm sieve were discarded. The plankton retained by each sieve was gently rinsed with filtered (64 μm) lake water into plastic bags for transport to the laboratory where we placed 2–6 replicate samples for each zooplankton size fraction and unsieved zooplankton (0.1–7 mg dry weight) on pieces of preweighed acid-washed Teflon sheeting that were frozen until Cd analysis. Remaining organisms were preserved in a 5% formalin solution for later identification and counting of crustacean zooplankton. In eight lakes having dense crustacean plankton communities (pH > 6.3, Table 3), we isolated copepods and cladocerans from bulk samples under a microscope for Cd measurements. Because of the large number of crustaceans (100–150) needed to make up a sample, we did not identify animals further. Individuals of each taxon were placed on preweighed acid-washed Teflon sheeting that was frozen until Cd analysis. We did not measure zooplankton Cd over several weeks before collecting *Chaoborus* (so as to integrate possible temporal changes in prey Cd) because unpublished data (Croteau) show that Cd concentrations in bulk plankton vary little over the 2 weeks that it takes *Chaoborus* larvae to achieve a steady state in their Cd concentrations in the early spring (Croteau et al. 2001, 2002). Furthermore, even if there were a drastic drop in zooplankton Cd, it would take a minimum of 3 weeks for *Chaoborus* to lose half of its Cd (Munger et al. 1999).

We collected water samples in 2–3 diffusion samplers (Croteau et al. 1998) that were suspended for 3 days in the epilimnion of each lake. On installation and retrieval dates,

Table 1. Study lake locations, pH, and concentrations of total dissolved organic carbon (C_{org}), Ca, and Cd.

Region and lake	Lake code	Location	pH	[C_{org}], mg $C\cdot L^{-1}$	[Ca], µM	[Cd], nM
Killarney, Ontario						
Terry*	TE	46°04′N, 81°17′W	4.56	7.9	37	0.9
Sudbury, Ontario						
Chief*	CH	46°22′N, 81°01′W	4.47	5.3	40	2.7
Crooked	CK	46°25′N, 81°02′W	5.07	3.6	74	4.5
Crowley	CW	46°23′N, 80°59′W	6.85	2.8	59	1.2
Daisy*	DY	46°27′N, 80°53′W	5.36	4.3	59	2.5
Forest	FO	46°23′N, 81°00′W	6.23	2.5	65	1.4
Hazen*	HA	46°25′N, 80°59′W	4.46	8.8	2237	3.3
Johnny	JH	46°26′N, 81°02′W	7.12	4.6	229	1.4
Pine*	PI	46°22′N, 81°02′W	4.30	6.0	30	3.8
Tilton	TI	46°22′N, 81°04′W	6.61	2.4	119	1.3
Rouyn-Noranda, Quebec						
Bousquet	BO	48°14′N, 78°34′W	6.35	12.1	97	0.85
Caron	CA	47°56′N, 78°58′W	7.01	11.3	288	0.89
Chevreuil*	CV	47°54′N, 79°00′W	4.50	5.2	29	2.5
d'Alembert	DA	48°23′N, 79°01′W	7.15	9.0	160	0.44
Desperiers*	DE	48°11′N, 79°09′W	5.16	5.6	42	3.2
Duprat	DU	48°20′N, 79°07′W	7.11	6.7	173	0.41
Flavrian	FL	48°18′N, 79°11′W	7.27	7.8	156	0.43
Hélène	HE	48°13′N, 79°10′W	8.05	8.9	420	0.07
Joannès	JO	48°11′N, 78°41′W	6.95	10.4	164	0.64
La Bruère	LA	48°10′N, 78°57′W	7.79	9.9	304	0.61
Marlon	MA	48°16′N, 79°04′W	7.35	8.6	138	1.18
Surimeau*	SU	48°08′N, 79°19′W	4.95	8.5	39	0.9
Turcotte*	TU	48°18′N, 79°04′W	4.83	5.4	105	19.5
Vaudray	VA	48°07′N, 78°42′W	6.65	7.8	81	0.57

Note: Water samples were collected from the epilimnion of each lake using in situ diffusion samplers.

*Data from Croteau et al. (1998).

we measured the pH in water samples collected with a van Dorn bottle at the depth of the diffusion samplers.

Analyses

To minimize inadvertent trace metal contamination, we soaked all labware and sampling material in 15% nitric acid and rinsed them in ultrapure water (>18 MΩ cm) before use. We measured total dissolved Cd concentrations by flameless atomic absorption spectrophotometry (AAS; THGA graphite tube atomiser, model SIMAA 6000 (Perkin-Elmer, Boston, Mass.)). Certified reference riverine water samples (National Research Council of Canada (NRCC); SLRS-4, National Institute of Standards and Technology, 1643d) were analyzed during each analytical run and measured trace metal concentrations were within the certified range. We measured calcium by flame AAS (Spectra AA-20; Varian Instruments, Walnut Creek, Calif.) and dissolved organic carbon using a total organic carbon analyser (TOC-5000A; Shimadzu, Columbia, Md.).

Chaoborus larvae and zooplankton samples were freeze-dried (FTS Systems, Stone Ridge, N.Y.), weighed on a microbalance (ME30; Mettler-Toledo, Columbus, Ohio), and digested in concentrated nitric acid (100 $\mu L\cdot mg^{-1}$ dry weight (DW); Aristar grade). For invertebrate samples collected in 1996 and 1997, we carried out digestions in thick-walled, screw-cap Teflon vials in an autoclave at 120°C for 3 h. Cooled digested samples were diluted to volume with ultrapure water. For samples collected in 1998, we conducted digestions at room temperature in 4-mL HDPE vials for 7 days. Hydrogen peroxide (40 $\mu L\cdot mg^{-1}$ DW) was added 24 h before final dilution with ultrapure water (760 $\mu L\cdot mg^{-1}$ DW). Cadmium values were comparable for the two digestion methods used. We submitted samples of similar weight of a certified reference material (lobster hepatopancreas, TORT-1, NRCC) to the same digestion procedure during each run. Cadmium concentrations in animal digests were analyzed by flameless AAS (Varian, Spectra AA-30); Cd concentrations measured for TORT-1 were within the certified range and the recovery of Cd in spiked samples was within 10% of the amount added. The software SYSTAT 10 (Systat Software, Richmond, Calif.) was used for all statistical analyses. We used linear regressions to relate Cd concentrations in *Chaoborus* to those in its potential prey, as well as to relate Cd measurements in zooplankton to those in lake water. Comparisons of Cd concentrations among plankton size fractions were made by *t* tests.

Results and discussion

Chaoborus larvae are reported to take up Cd mainly from the zooplankton that they consume as prey (Munger and Hare 1997; Munger et al. 1999). Thus we might expect that at steady-state Cd concentrations in this predator, $[Cd]_{Chaoborus}$, would be directly related to those in its prey, $[Cd]_{zooplankton}$, that is,

Table 2. Mean Cd concentrations ($\mu g \cdot g^{-1}$ dry weight; ± standard deviation) in bulk and size-fractionated zooplankton samples, as well as in various *Chaoborus* species from our study lakes.

	Plankton Cd concentrations				*Chaoborus* species Cd concentrations			
Region and lake	Bulk	500–1000 µm	300–500 µm	64–300 µm	*punctipennis*	*albatus*	*flavicans*	*americanus*
Killarney, Ontario								
Terry*	0.72±0.02 (3)	0.64±0.06 (3)	0.50±0.03 (3)	1.0±0.1 (3)	1.9±0.1 (5)	NP	NP	NP
Sudbury, Ontario								
Chief*	1.2±0.3 (3)	INS	2.7±0.2 (3)	0.45±0.02 (3)	1.5±0.1 (4)	NP	NP	NP
Crooked†	1.4±0.3 (3)	3.9±3 (2)	1.1±0.2 (2)	0.46±0.01 (3)	3.2±0.3 (5)	3.8 (1)	4.0±0.4 (2)	4.0±0.2 (5)
Crowley†	4.1±0.5 (4)	3.8±0.5 (3)	1.5±0.2 (4)	2.2±0.3 (3)	10.9±0.3 (5)	NP	8.6±0.5 (5)	NP
Daisy*	2.8±0.4 (3)	INS	2.1±0.01 (3)	3.4±0.01 (3)	2.8±0.3 (5)	NP	NP	NP
Forest†	2.5±0.7 (4)	6.2±0.4 (4)	3.4±0.1 (4)	1.2±0.1 (4)	8.3±0.4 (5)	NP	4.9±0.2 (5)	NP
Johnny†	3.4±0.5 (3)	1.5±0.3 (2)	1.0±0.4 (2)	4.0±0.3 (3)	11.9±0.8 (5)	NP	NP	13.6±0.9 (5)
Hazen*	2.2±0.1 (3)	INS	3.4±0.9 (3)	2.0±0.1 (3)	1.1±0.1 (5)	NP	1.6±0.1 (5)	2.6±0.4 (5)
Pine*	2.1±0.1 (3)	INS	1.3±0.1 (3)	2.3±0.1 (3)	3.9±1.1 (3)	3.4±0.2 (5)	NP	NP
Tilton†	3.7±0.3 (4)	0.81±0.1 (3)	0.46±0.04 (3)	1.5±0.3 (4)	7.6±1.0 (5)	NP	6.6±0.6 (5)	NP
Rouyn-Noranda, Quebec								
Bousquet†	2.0±0.1 (4)	0.95±0.03 (4)	0.72±0.4 (4)	0.34±0.03 (4)	2.0±0.2 (5)	NP	3.0±0.4 (5)	NP
Caron	3.9±0.5 (4)	1.0±0.1 (4)	0.36±0.1 (4)	0.24±0.06 (4)	5.6 (1)	NP	4.8±0.4 (5)	NP
Chevreuil*	2.1±0.2 (3)	INS	0.43±0.06 (3)	0.37±0.05 (5)	1.5 (1)	NP	NP	3.0±0.5 (5)
d'Alembert‡	8.1±1.1 (4)	4.3±0.4 (4)	2.7±0.1 (4)	1.1±0.04 (4)	2.3 (1)	NP	1.7±0.1 (5)	NP
Desperiers*	3.9±0.3 (5)	5.3±0.5 (5)	2.3±0.03 (5)	1.4±0.1 (5)	1.1±0.2 (5)	NP	2.8±0.4 (5)	NP
Duprat†	2.2±0.1 (4)	1.7±0.2 (4)	0.96±0.04 (4)	0.36±0.01 (4)	1.4±0.1 (5)	NP	1.3±0.2 (5)	NP
Flavrian§	3.6±0.2 (3)	7.0±0.1 (4)	1.8±0.2 (3)	1.5±0.1 (4)	NP	1.3±0.1 (5)	NP	NP
Hélène	ND	ND	ND	ND	0.13±0.02 (3)	0.18±0.04 (3)	NP	NP
Joannès	5.0±0.1 (4)	3.4±0.3 (4)	3.1±0.2 (4)	0.69±0.02 (4)	NP	NP	3.6±0.2 (5)	NP
La Bruère‡	3.2±0.3 (4)	2.5±0.1 (4)	2.5±0.1 (4)	0.44±0.04 (4)	1.7±0.1 (5)	NP	NP	NP
Marlon†	43±14 (4)	41±3 (4)	28±2 (4)	1.8±0.2 (4)	5.6±0.6 (4)	4.9±0.5 (4)	NP	NP
Surimeau*	33±2 (5)	8.5±1.8 (6)	2.3±0.3 (5)	29±3 (5)	2.7±0.2 (5)	NP	1.3±0.1 (3)	NP
Turcotte*	2.7±0.2 (3)	INS	2.0±0.1 (2)	4.1±1.2 (3)	3.1±0.1 (5)	NP	NP	9.9±0.8 (5)
Vaudray†	3.0±0.5 (4)	4.2±0.3 (4)	3.3±0.3 (4)	0.39±0.05 (4)	2.9±0.1 (2)	NP	4.5±0.3 (5)	NP

Note: All zooplankton samples (including *Chaoborus*) were collected on a single date over a short time period (late May to mid-June) in the spring. Sample numbers are given in parentheses. INS, insufficient number of organisms; NP, not present; ND, not determined.

**Chaoborus* data from Croteau et al. (1998).

†*Chaoborus* data from Croteau et al. (2001).

‡*Chaoborus punctipennis* data from Croteau et al. (2002).

§*Chaoborus* data from Croteau et al. (2002).

Table 3. Mean Cd concentrations ($\mu g \cdot g^{-1}$; ± standard deviation) in copepods and cladocerans, as well as the ratio of their densities in the 64- to 300-µm size fraction of plankton collected from lakes in the region of Rouyn-Noranda, Quebec.

Lake	$[Cd]_{copepods}$	$[Cd]_{cladocerans}$	Abundance ratio copepods:cladocerans
Bousquet	0.99±0.1 (3)*	0.89 (1)	1.2
d'Alembert	3.1±0.4 (3)*	4.2±0.5 (4)	11
Duprat	1.6±0.1 (3)*	1.3±0.05 (2)	20
Flavrian	2.0 (1)*	5.5±0.4 (3)	3.3
Hélène	1.1±0.2 (5)*	0.99±0.4 (3)	1†
Joannès	2.9±1 (4)	0.75±0.2 (2)	31
La Bruère	2.9±0.5 (3)*	1.6±0.3 (3)	54
Marlon	23±2 (2)	20±2 (3)	8.2
Vaudray	5.8±0.2 (3)*	3.2±0.4 (2)	26

Note: Sample numbers are given in parentheses.

*Data from Croteau et al. (2002).

†We assumed a 1:1 ratio because Cd concentrations in cladocerans and copepods from this lake were not significantly different.

$$[Cd]_{Chaoborus} = F_{Chaoborus\text{–}zooplankton} \times [Cd]_{zooplankton} \quad (1)$$

where $F_{Chaoborus\text{–}zooplankton}$ is a proportionality constant.

Bulk plankton as prey

We tested eq. 1 with data from 23 lakes in which we measured Cd in *Chaoborus* larvae and in bulk plankton (Table 2); rotifers (mainly *Keratella*) were the numerically dominant animal group in these plankton samples (Fig. 2*a*, inset). There were no significant relationships ($P > 0.05$) between Cd concentrations in bulk zooplankton and those in *Chaoborus* larvae, regardless of whether data were pooled at the generic level (i.e., *Chaoborus*, not shown) or treated on a species by species basis (e.g., *C. punctipennis*; Fig. 2*a*). Furthermore, no significant relationships emerged if we excluded two high-Cd values for zooplankton (lakes MA and SU in Fig. 2*a* and Table 2). This lack of a relationship between Cd concentrations in the predator and in bulk samples of potential prey does not signify that eq. 1 is invalid, but is more likely a consequence of the fact that the predator does not consume all sizes and types of prey in bulk zooplankton. This postulate is supported by the fact that Cd concentrations in *Chaoborus* substantially exceeded those in bulk zooplankton in several circumneutral lakes (open symbols in Fig. 2*a*) in the Sudbury area (Table 2), whereas Cd concentrations in invertebrate predators should be lower than those in their prey (Hatakeyama and Yasuno 1987; van Hattum et al. 1989; Croteau et al. 2001).

Size fractions of zooplankton as prey

Because *Chaoborus* larvae are limited by the gape of their mouth to prey below a certain size (Hare and Carter 1987), we fractionated bulk plankton samples into three size classes. The largest size fraction (500–1000 µm) would be unavailable to fourth instars of our small-sized study species, *C. punctipennis* and *C. albatus* (mouth gapes ≈ 450 µm; Moore 1988), and available only in part to the large-sized species, *C. flavicans* (mouth gape ≈ 630 µm; Stenson 1980) and *C. americanus* (mouth gape ≈ 700 µm; Fedorenko 1975). Prey in the two smaller size fractions (300–500 and 64–300 µm) should be available to all of these *Chaoborus* species. Crustaceans (copepods and cladocerans) dominated numerically the larger size fractions (Figs. 2*b*–2*c*, insets), whereas rotifers dominated the smallest size fraction (Fig. 2*d*, inset). Again, there were no significant relationships ($P > 0.05$) between Cd concentrations in any zooplankton size fraction and those in *Chaoborus* at either the genus (not shown) or the species level (e.g., *C. punctipennis*; Figs. 2*b*–2*d*). In addition, no significant relationships emerged when we excluded extreme zooplankton values (MA and SU in Figs. 2*b*–2*d*).

This lack of correlation is especially evident for the highly acidic lakes (Fig. 2, solid circles) in which Cd concentrations in *Chaoborus* are consistently low in spite of large differences in zooplankton Cd among these lakes. One possible explanation for this trend is that if *Chaoborus* larvae take in sufficient lake water to influence midgut pH (unknown at present), then hydrogen ions could outcompete Cd ions from prey at biological uptake sites in the predator's gut leading to lower Cd concentrations in larval tissues. Competition between hydrogen and Cd ions has been invoked as an explanation for the generally low Cd concentrations measured in *Chaoborus* larvae from highly acidic lakes (Croteau et al. 1998). A second possible explanation for the uniformly low Cd concentrations in *Chaoborus* from highly acidic lakes is that there is a scarcity of the crustacean prey preferred by *Chaoborus* in these lakes (Havens and Hanazato 1993; Locke et al. 1994). In such lakes, *Chaoborus* larvae would be limited to feeding largely on rotifers, which, given their small mass, would result in reduced prey ingestion rates and low predator mass for a given body length (Havens and Hanazato 1993). Reduced predator mass with decreasing pH is supported by data for final instar *C. punctipennis* from a large number of lakes (Fig. 3, $P < 0.001$, $r^2 = 0.57$). Feeding studies on *C. punctipennis* in one of our highly acidic lakes (Turcotte, pH 4.83) confirm that final instar larvae have a small mass (Fig. 3, TU), feed largely on rotifers (Croteau et al. 2003), and are low in Cd in spite of the high dissolved Cd concentrations in this lake (Tables 1 and 2; Croteau et al. 1998). Because *Chaoborus* in highly acidic lakes have a smaller range of prey types from which to choose (Havens and Hanazato 1993; Locke et al. 1994), our measurements of Cd in zooplankton from acidic lakes are likely to be more representative of prey actually eaten by *Chaoborus* than are those on zooplankton from circumneutral lakes. This appears

Fig. 2. Relationships between mean (± standard deviation; $\mu g \cdot g^{-1}$ dry weight) Cd concentrations in final instar larvae of *Chaoborus punctipennis* and (*a*) samples of bulk zooplankton >64 μm, (*b*) the 500- to 1000-μm zooplankton size fraction, (*c*) the 300- to 500-μm zooplankton size fraction, and (*d*) the 64- to 300-μm zooplankton size fraction (solid symbols, pH < 5.5; open symbols, pH > 5.5). Each point corresponds to a particular lake (MA, Marlon; SU, Surimeau). Inset pie graphs illustrate the mean relative numbers of major zooplankton groups for all lakes: solid, copepods; shaded, rotifers; open, cladocerans.

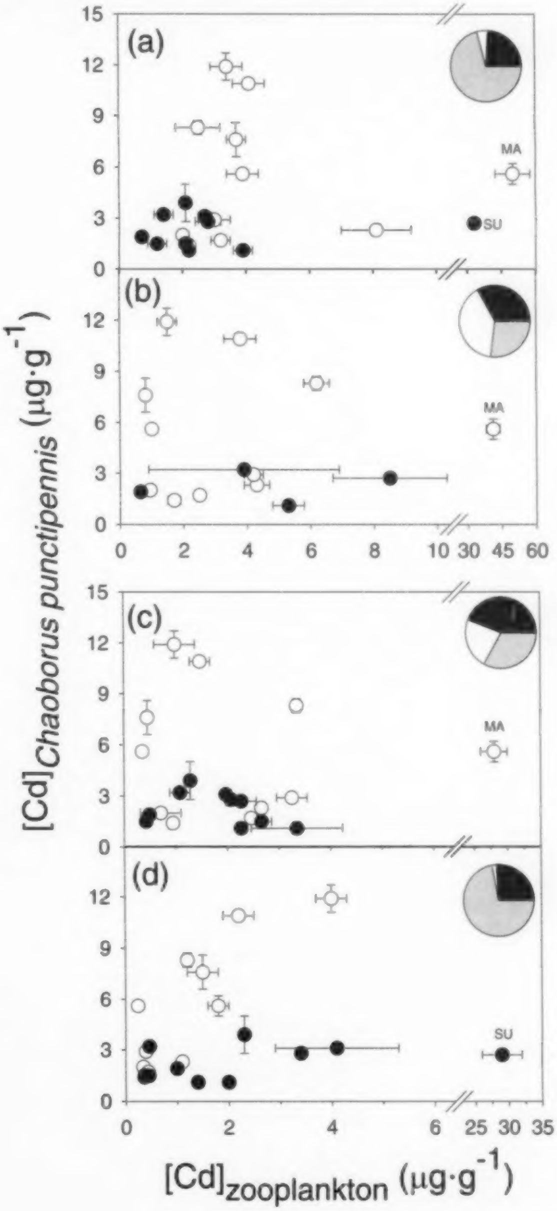
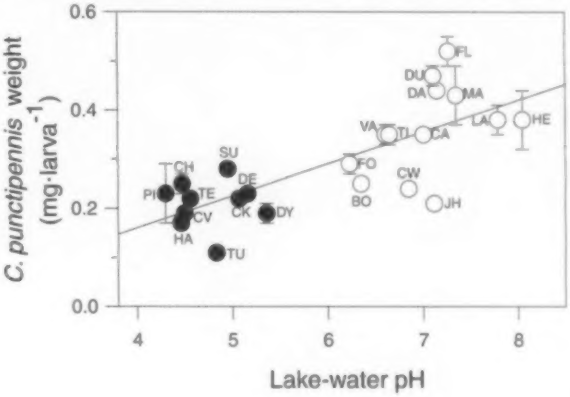


Fig. 3. Mean weight of final instar larvae of *Chaoborus punctipennis* (± standard deviation; mg dry weight·larva^{-1}) as a function of lake-water pH (solid symbols, pH < 5.5; open symbols, pH > 5.5). Each point corresponds to a particular lake: BO, Bousquet; CA, Caron; CH, Chief; CK, Crooked; CV, Chevreuil; CW, Crowley; DA, d'Alembert; DE, Desperiers; DU, Duprat; DY, Daisy; FL, Flavrian; FO, Forest; HA, Hazen; HE, Hélène; JH, Johnny; JO, Joannès; LA, La Bruère; MA, Marlon; PI, Pine; SU, Surimeau; TE, Terry; TI, Tilton; TU, Turcotte; VA, Vaudray.



to be the case because Cd concentrations in *Chaoborus* from some circumneutral lakes greatly exceeded those in zooplankton (which should not be the case; Hatakeyama and Yasuno 1987; van Hattum et al. 1989; Croteau et al. 2001), whereas Cd concentrations in *Chaoborus* from highly acidic lakes did not. Although we reason above in terms of the types of prey and their rates of ingestion, a lower efficiency of Cd assimilation from rotifers than from crustaceans could also potentially contribute to the lower Cd concentrations in *Chaoborus* from highly acidic lakes (Reinfelder et al. 1998; Croteau et al. 2001); at present there is no information on assimilation efficiencies of these elements by predators from rotifers that we could use to judge the importance of this variable.

We also used our size-fraction data to test the supposition that zooplankton size fractions represent different trophic levels, with increasing animal size being equated to increasing trophic level (Chen and Folt 2000; Chen et al. 2000). If this were the case, then we would expect that Cd concentrations should decline with increasing animal size because concentrations of this metal decrease with increasing trophic level (Hatakeyama and Yasuno 1987; van Hattum et al. 1989; Croteau et al. 2001). Our data do not support this idea because Cd concentrations in the smallest size fraction were significantly lower ($P < 0.05$) than those in the two larger size fractions in 12 of 17 lakes from which we obtained all size fractions (Table 2). Knowledge of feeding habits would also argue against such a trend; the widespread microcrustacean *Daphnia*, although mainly herbivorous, is larger than most omnivorous planktonic microcrustaceans (Dodson and Frey 1992). To unambiguously demonstrate trophic trends in metal concentrations, we suggest using measurements of stable N-isotope ratios to compare the relative trophic heights of purported food chain links (France et al. 1996).

Fig. 4. Relationships between mean (± standard deviation; $\mu g \cdot g^{-1}$ dry weight) Cd concentrations in final instar larvae of three *Chaoborus* species and their potential (*a*) cladoceran or (*b*) copepod prey. ○, *C. punctipennis*; △, *C. albatus*; □, *C. flavicans*.

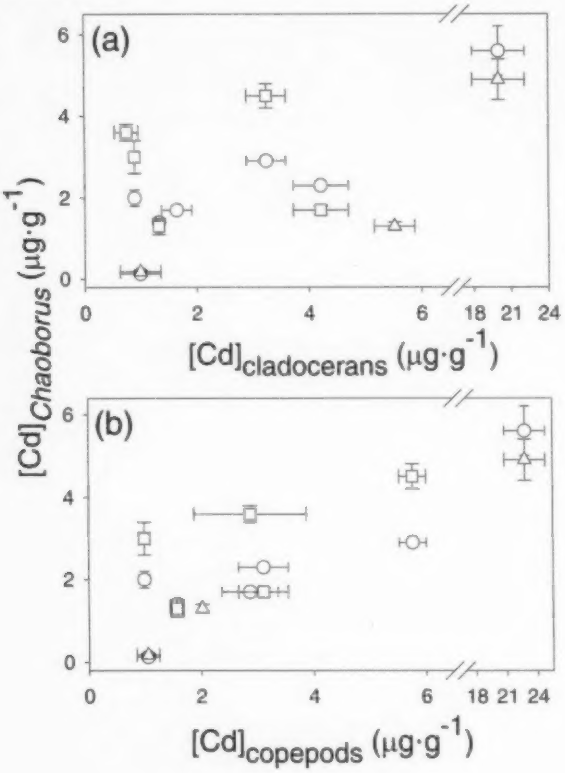
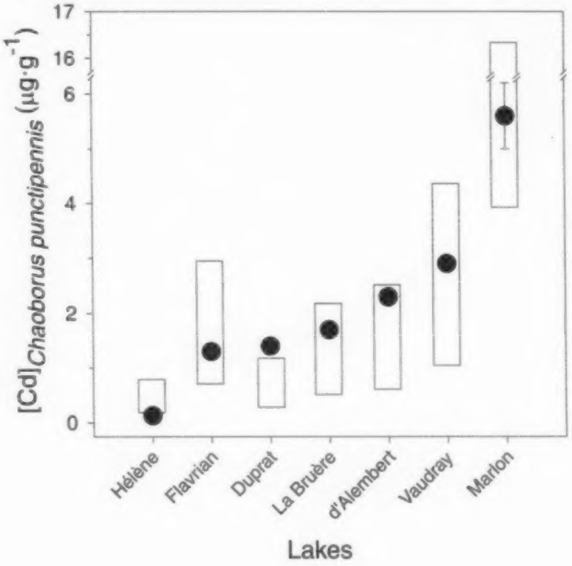


Fig. 5. Measured Cd concentrations (mean ± standard deviation; $\mu g \cdot g^{-1}$ dry weight) in final instar larvae of *Chaoborus punctipennis* collected from various lakes (●) compared with model predictions for Cd concentrations in this predator at 5 and 22°C (bars). Error bars are too small to be visible for all lakes except Lake Marlon. Predicted Cd values for *C. punctipennis* were estimated for each temperature using eq. 2 and the parameters AE, IR, k_g, k_e (obtained from Croteau et al. 2002), and $[Cd]_{Food}$ (abundance weighted mean of Cd concentrations measured in copepods and cladocerans from each lake). Upper and lower edges of bars correspond to model predictions at 22 and 5°C, respectively. Data for Lake Flavrian are for the closely related species *Chaoborus albatus*.



Crustacean zooplankton as prey

Sieving zooplankton into size categories suitable for *Chaoborus* ingestion is inefficient because it likely traps some zooplankton on their side, that is, according to their length rather than their width. However, because *Chaoborus* larvae orient captured prey so as to swallow them head-on, it is likely that prey width is a better determinant of successful ingestion than is prey length (Moore and Gilbert 1987). This could explain in large part the lack of relationships that we found between Cd concentrations in *Chaoborus* and those of size-fractionated zooplankton prey (Figs. 2*b*–2*d*). To better isolate prey of a suitable size and prey types known to be consumed by *Chaoborus* (Swüste et al. 1973; Moore 1988), we hand-picked suitable-sized cladocerans and copepods from a subset of our study lakes in which numbers of large-bodied crustaceans were sufficient to permit their removal by hand and their aggregation into samples of sufficient biomass for Cd analyses (Table 3, circumneutral lakes). Although Cd concentrations in cladocerans and copepods were directly related ($P < 0.05$) to those of *Chaoborus* (Figs. 4*a*–4*b*), these relationships depend on the high Cd values in animals from a single lake (Lake Marlon, Table 3), which are in turn a consequence of the higher total dissolved Cd concentrations in this circumneutral lake compared with those of the other lakes in Fig. 4 (Table 1). To better determine if our Cd measurements in these prey types could be used to predict those in the predator, we incorporated these measurements into a mechanistic bioaccumulation model (Croteau et al. 2001, 2002) to determine if the laboratory-derived constants in such a model would permit prediction of [Cd] in *Chaoborus* collected in nature. Steady-state Cd concentrations in the predator, $[Cd_{Chaoborus}]_{ss}$, can be predicted (Croteau et al. 2001, 2002) from Cd concentrations in its planktonic food, $[Cd]_{Food}$, given temperature-specific values for the efficiency with which the predator assimilates this metal (AE), the rate at which it ingests its prey (IR), as well as rate constants for Cd loss (k_e) and larval growth (k_g), that is,

$$(2) \qquad [Cd_{Chaoborus}]_{ss} = \frac{AE \times IR \times [Cd_{Food}]}{k_e + k_g}$$

Using values of AE, IR, k_e, and k_g estimated for *C. punctipennis* by Croteau et al. (2002) along with our values for Cd in potential crustacean prey from each lake (based on mean Cd concentrations in copepods and cladocerans weighted for their relative densities in the size fraction available to the predator (64–300 µm; Table 3)), we predict Cd concentrations in this predator for the extremes of temperature that it is likely to encounter in nature (5 and 22°C). Because Cd concentrations in this predator are reported to be inferior to those of its prey (Munger et al. 1999; Croteau et al. 2001, 2002), we excluded data for one lake (Bousquet) in which predator Cd concentrations exceeded those measured in planktonic crustaceans (Table 3). To verify that this assumption is justified, we used the bioaccumulation model described in eq. 2 to determine under what circumstances $[\mathrm{Cd}_{Chaoborus}]_{ss}/[\mathrm{Cd}]_{prey}$ exceed 1; all such scenarios imply the use of biologically unrealistic values of at least one model constant (AE, IR, k_e, or k_g). The results of these model simulations suggest that if Cd concentrations in bulk or size-fractionated zooplankton are lower than those in *Chaoborus*, then it is likely because these gross prey assemblages include a majority of individuals that are not a major component of this predator's diet.

Measured predator Cd values fall close to or within model predictions for most lakes (Fig. 5), suggesting that this model provides a rough tool for predicting Cd concentrations in *C. punctipennis* from those in its crustacean prey. Identifying prey below groupings such as "copepods" would likely improve model predictions further. For example, we measured substantial differences in the Cd concentrations (means ± 95% confidence interval (CI) in $\mu g \cdot g^{-1}$) of two calanoid copepods collected from one of our study lakes (L. Caron), that is, *Limnocalanus macrurus* (2.9 ± 0.1), which is too large to be eaten by *Chaoborus*, and *Diaptomus* sp. (5.5 ± 1.0), which are eaten by this insect. When we used values for Cd in bulk or size-fractionated prey in eq. 2, measured data points usually fell outside of the range expected from model predictions (figures not shown), suggesting that finer prey taxonomic resolution will aid in predicting predator Cd.

In conclusion, a relationship between Cd concentrations in *Chaoborus* and those in its prey is to be expected given that the Cd in *Chaoborus* comes entirely from its prey (Munger and Hare 1997; Munger et al. 1999). However, our attempts to relate metal concentrations in this planktonic predator to those in its prey met with mixed success; although we observed no relationship between Cd concentrations in *Chaoborus* and those in bulk or size-fractionated zooplankton samples, a positive relationship was observed between Cd concentrations measured in specific prey taxa and those predicted in *Chaoborus* by a bioaccumulation model. We suggest that predictions of metal concentrations between adjacent links in food chains, as well as trends in metal concentrations along food chains, are likely to be unreliable if they are based on metal measurements in samples of poorly identified bulk prey and if there is a lack of knowledge of the prey actually consumed by the predator living in planktonic communities composed of different mixtures of prey types. Field measurements of metals in well-defined planktonic food chains are needed to better understand metal trophic transfer in nature.

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Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*)

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Abstract: Fisheries scientists and managers are concerned about potential long-term, persistent changes in productivity of fish stocks that might result from future climatic changes or other alterations in aquatic systems. However, because of large natural variability and measurement error in fisheries data, such changes are usually difficult to detect until long after they occur. Previous research using numerous Monte Carlo simulation trials showed that a Kalman filter performed better than standard estimation techniques in detecting such trends in a timely manner. Therefore, we used historical data along with a Kalman filter that included a time-varying Ricker *a* parameter to reconstruct changes in productivity (recruits per spawner at a given spawner abundance) of eight Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*) stocks over the past 40 years. Productivity generally increased for most stocks but varied widely for others and dramatically decreased in another. Such large changes in productivity are important for management. They greatly affected optimal spawner abundances and optimal exploitation rates, suggesting that in the future, scientists should consider using models with time-varying productivity parameters.

Résumé : Les biologistes et les gestionnaires des pêches se préoccupent des changements potentiels permanents et à long terme dans la productivité des stocks de poissons qui peuvent résulter des changements climatiques futurs ou d'autres modifications des systèmes aquatiques. Cependant, à cause de la forte variabilité naturelle et des erreurs de mesure dans les données sur les pêches, de tels changements sont difficiles à déceler et souvent ne le sont que longtemps après leur apparition. Des travaux antérieurs qui ont utilisé de nombreux essais de simulations de Monte Carlo ont montré qu'un filtre de Kalman permettait de reconnaître ces changements plus efficacement et dans un intervalle de temps plus court que les méthodes habituelles d'estimation. Nous utilisons donc des données du passé avec un filtre de Kalman qui comprend un paramètre *a* de Ricker variable dans le temps pour représenter les changements dans la productivité (nombre de recrues par reproducteur à une abondance donnée de reproducteurs) de huit stocks de saumons rouges (*Oncorhynchus nerka*) de la baie de Bristol, en Alaska, au cours des 40 dernières années. En général, la productivité augmente chez la plupart des stocks, elle est très variable chez d'autres et elle connaît une chute spectaculaire chez l'un d'eux. Des changements d'une telle importance dans la productivité sont d'un grand intérêt pour les gestionnaires. Ils affectent l'abondance optimale des reproducteurs et le taux optimal d'exploitation, ce qui fait croire que, dans l'avenir, les biologistes devraient envisager l'utilisation de modèles où figurent des paramètres de productivité variables dans le temps.

[Traduit par la Rédaction]

Introduction

Fisheries scientists and managers are concerned about potential long-term, persistent changes in productivity of fish stocks that might result from future climatic changes or alterations in habitat, food supply, or predators. Such "trends in productivity" — a phrase used in this paper to broadly characterize any systematic changes in recruits produced per spawner or per unit spawning biomass at a given spawner abundance — have been discussed in the recent fisheries literature using various terms. These include low-frequency variability, regime shifts, decadal-scale variability, autocorrelation, and nonstationarity in productivity. Whatever their form, trends in productivity have important implications for management and industry (Walters 1987). In contrast to the short-term implications of rapid, year-to-year variability, trends in productivity may have profound long-term consequences for sustainable harvest rates and associated economic and social benefits. For example, during periods of low

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productivity, it may be critical that proportional harvest rates are lowered to reduce risks and increase the chance that fish stocks will persist.

Concerns about trends in productivity have been stimulated by observations of large changes in abundance indices of many fish stocks over periods of several years or more. Such changes may reflect the effect of harvesting, as well as changes in oceanographic conditions (Bakun 1996; Kawasaki 1991), food supply, predation, or other factors. For example, multi-decade-long periods of high and low sockeye salmon (*Oncorhynchus nerka*) abundance of the Karluk Lake (Alaska) stock have occurred during the last 2200 years, based on stable isotope analysis of sediment cores (Finney et al. 2000, 2002). As well, other species have shown large changes in abundance indices over the last 2000 years, long before fishing by humans began. The best known cases are for California sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) (Baumgartner et al. 1992; Jacobson and MacCall 1995). In addition, some authors have used catch data to contend that numerous Northeast Pacific salmon (*Oncorhynchus* spp.) stocks experienced multi-decade-long periods of high and low productivity in the 1900s as a result of climatic forcing (Hare et al. 1999).

To account for trends in productivity, which may have contributed to the above changes in abundance, researchers have developed models of population dynamics that assume time-varying productivity parameters (e.g., Walters 1986; Pella 1993; Walters and Parma 1996). However, these models have not been widely used in analyses of Pacific salmon stocks for at least two reasons. The first is pragmatic. Most researchers and managers probably do not recognize that such models are necessary. It is difficult to detect changes over time in the parameters of stock–recruitment curves because of relatively short data sets, large natural variability, and measurement errors. For instance, almost all analyses of Pacific salmon stocks use the Ricker (1975) stock–recruitment model and assume that its a and b parameters are constant over the entire data set. In some situations, researchers go one step further by partitioning their data into different blocks, which are assumed to represent periods of different productivity (e.g., pre- and post-1976 for analyses of sockeye salmon in Bristol Bay, Alaska; Hal Geiger, Alaska Department of Fish and Game, P.O. Box 25526, Juneau, AK 99801, personal communication). However, because of the large variability in typical data sets, such periods are only recognizable well after a change in productivity occurs (Adkison et al. 1996; Peterman et al. 1998). This does not help managers adjust their harvest strategies in a timely manner as productivity changes.

The second reason for the lack of wider use of models with time-varying parameters is that their performance at reflecting real changes in parameters has only recently been examined using comprehensive Monte Carlo simulations (Peterman et al. 2000). That analysis demonstrated that if the Ricker a parameter varies over time, a Kalman filter (state–space) formulation of the Ricker model with a time-varying a parameter performs better at tracking those changes than the standard Ricker model, which assumes that parameters are constant (Peterman et al. 2000). This superior parameter estimation of the Kalman filter approach held across a wide variety of simulated trends in the Ricker a parameter for a salmon stock (e.g., step function, sine wave, autoregressive process). Consequently, the Kalman filter produced more accurate and precise estimates of the optimal number of spawners as the optimum changed over time than did either the standard linear regression estimation method for the Ricker model or Walters' (1990) bias correction to that method (Peterman et al. 2000).

This superiority of the Kalman filter formulation arises from its explicit partitioning of the observed variation in $\log_e$(recruits/spawner) into systematic changes over time in productivity (i.e., the "signal") and random sources of variation that are independent of that trend (see Materials and methods). Thus, in contrast to traditional stock–recruitment models, the Kalman filter approach helps deal with one of the biggest challenges faced by fisheries scientists and managers when trying to detect changes in fish productivity, namely, separating important temporal trends from less important interannual variation. In general, managers need to respond to such trends in productivity by altering harvest or escapement goals, whereas responding to interannual variation would result in chasing "noise" rather than the underlying "signal".

In this paper, we applied the Kalman filter approach to data for eight Bristol Bay sockeye salmon stocks to reconstruct trends in their productivity over the past 40 years. Previous analyses indicate that these stocks experienced large and persistent increases in productivity beginning in the mid-1970s (Adkison et al. 1996; Peterman et al. 1998). There is currently some debate over whether these stocks might have recently moved back to a less-productive regime. Our purpose was to use trends in productivity estimated by the Kalman filter approach to address the following questions. (1) What are the characteristics of trends in productivity in these Bristol Bay sockeye salmon stocks (e.g., magnitude and rate of changes)? (2) Are these characteristics similar across stocks? (3) What do estimated trends in productivity imply about changes in optimal abundance of spawners and optimal harvest rates? (4) Do these trends correspond with the widely studied "regime shift" in the mid-1970s in the Northeast Pacific Ocean? (5) Is there any evidence of more recent regime shifts? To estimate trends in productivity, we used two different forms of the Ricker model cast in the Kalman filter framework. In addition, we compared results for these two models with results based on the standard Ricker model.

Materials and methods

Data

We used age-specific abundances of spawners and adult recruits (catch plus spawning escapement) for the eight main Bristol Bay sockeye salmon stocks in Alaska (Branch, Egegik, Igushik, Kvichak, Naknek, Togiak, Ugashik, and Wood) from brood years 1956 through 1995, the latest brood year for stocks with complete data on 6-year-old recruits (Lowell Fair, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AL 99518, personal communication). We used the entire data set for each stock except the Kvichak River stock, which has large variations in abundance (over two orders of magnitude). Although this provided large contrast in the data, there was no evidence of density dependence for the Kvichak stock in any stock–recruitment models that we examined (positive Ricker *b* parameter in eqs. 1 and 3 below). This created an upward curving stock–recruitment curve with an undefined optimal escapement and optimal harvest rate. For the purpose of this paper, we avoided this problem by omitting 3 years from the Kvichak data set (the 1960, 1965, and 1970 brood years, the last 3 years of the so-called "dominant cycle line" before the mid-1970s shift in productivity). These brood years had extremely large abundances of spawners and recruits relative to the intervening brood years. Given the large natural variability in survival rates, this small sample of three influential brood years masked evidence of density dependence. As noted below, this procedure made little difference to our reconstructed trends in productivity compared with using all data for the Kvichak stock, yet allowed us to compute estimates of optimal escapements.

Alternative models

We used three alternative stock–recruitment models. These were variations on the Ricker (1975) stock–recruitment model, which is almost universally used in studies of Pacific salmon. The first model was the standard Ricker model:

$$(1) \qquad \log_e(R_t/S_t) = a + bS_t + u_t$$

where S_t is abundance of spawners in brood year *t*, R_t is abundance of adult recruits of all ages produced by those spawners (i.e., the brood-year recruits), *a* is the mean productivity (in units of $\log_e(R/S)$) at low spawner abundance, and *b* reflects the effects of spawner abundance on productivity (i.e., density dependence). Typically, the residual errors (u_t) are assumed to be independently and normally distributed with mean zero and variance σ_u^2. However, there was widespread evidence of autocorrelation in these residuals across stocks (e.g., Korman et al. 1995), thus violating the assumption of independence. To account for this autocorrelation, we modeled u_t as a first-order autoregressive (AR(1)) process:

$$(2) \qquad u_t = \phi u_{t-1} + \varepsilon_t$$

where ϕ is the autocorrelation coefficient and the errors (ε_t) are independently and normally distributed with mean zero and variance σ_ε^2. For an AR(1) process, $\sigma_u^2 = \sigma_\varepsilon^2/(1 - \phi^2)$. We refer to eqs. 1 and 2 together as the "standard Ricker" model. For that model, the parameters *a* and *b* are assumed to be constant over time.

Second, we formulated a Kalman filter "random-walk" (KF-RW) model to estimate parameters of the Ricker model. Kalman filter models are an example of the broad class of "state–space" models (Chatfield 1989); they consist of two parts. First, in our case, the "observation equation" (Chatfield 1989) describes the relationship between the observed quantities R_t and S_t:

$$(3) \qquad \log_e(R_t/S_t) = a_t + bS_t + v_t$$

This equation differs from eq. 1 in one important way: the *a* parameter is subscripted by brood year to reflect changes over time in productivity, as governed by a second stochastic process. The second part of the Kalman filter, the "system equation" (Chatfield 1989), describes how the *a* parameter varies over time; here it is a random walk:

$$(4) \qquad a_t = a_{t-1} + w_t$$

The error terms v_t and w_t in eqs. 3 and 4 are assumed to be normally distributed and independent, with variances σ_v^2 and σ_w^2, respectively. We used a simple, yet flexible, random walk in eq. 4 because no one knows the true temporal pattern of changes that have occurred in a_t. However, as shown by the theoretical analyses in Peterman et al. (2000), a random walk can perform well at tracking a wide variety of true underlying temporal trends in a_t. We formulated the KF-RW model (eqs. 3 and 4) to have a time-varying *a* parameter because Adkison et al. (1996) found that this parameter changed dramatically from the pre-1976 to the post-1976 period for most Bristol Bay sockeye stocks, whereas the Ricker *b* parameter did not. Furthermore, the only simulation study done to date evaluating the performance of various parameter-estimation techniques (Peterman et al. 2000) did so in the context of a temporal trend in the a_t parameter, and the KF-RW model performed the best.

The third model was also a Kalman filter model, but with a system equation in which a_t followed an AR(1) process (e.g., Zeng et al. 1998):

$$(5) \qquad a_t = \bar{a} + \phi\,(a_{t-1} - \bar{a}) + w_t$$

where $\bar{a}$ is the long-term mean for a_t. We refer to eqs. 3 and 5 together as the "KF-AR(1)" model. Equations 4 and 5 are equivalent when $\phi = 1$, hence the KF-RW model is a special case of the KF-AR(1) model. The standard Ricker model is also a special case of the KF-AR(1) model. This can be seen by substituting eq. 5 into eq. 3 and eq. 2 into eq. 1; when $\sigma_v^2 = 0$, $\bar{a} \equiv a$, and $w_t \equiv \varepsilon_t$. Thus, although both the standard Ricker model and the Kalman filter model can be formulated to include an AR(1) process, the key distinction is that the Kalman filter model explicitly separates variation in $\log_e(R/S)$ into variation in a_t (e.g., eq. 5) and random variation (v_t; eq. 3) that is independent of the process governing a_t.

Finally, although the observation-equation error (v_t) can account for both natural sources of random variation in $\log_e(R/S)$ and variation due to measurement error, this formulation does not explicitly model measurement error in spawner abundances (*S*) in eq. 3. Methods such as Kalman filtering and the "errors-in-variables" approach can be used to incorporate measurement error in *S* (e.g., Schnute and Kronlund 2002); however, these approaches require specification of the measurement-error variance. Because levels of measurement error in estimates of spawner abundance are not known for the Bristol Bay sockeye stocks examined here, we did not explicitly model this process.

Reconstruction of historical trends in productivity

To derive historical time series of productivity, we fit the three forms of the Ricker model to each of the eight spawner–recruit data sets. For the standard Ricker model, parameters were estimated via maximum likelihood. For this constant-parameter model, the time series of residual errors (u_t in eq. 1) provides estimates of changes in productivity over time (e.g., Peterman et al. 1998).

In contrast to the time series of u_t, which reflects all sources of residual variation (rapid changes, trends, and measurement error) in $\log_e(R_t/S_t)$, the Kalman filter models attempt to isolate systematic changes in productivity through the estimation of a_t. Details of the estimation procedures for the Kalman filter models are provided in Appendix A. In brief, the Kalman filter procedure recursively estimated a_t each year based on the previous year's estimate, a_{t-1}, and the new observation of $\log_e(R_t/S_t)$. In the first year only, we used a diffuse prior distribution for the initial estimate, a_1, with an arbitrary prior mean of 1.0 and a variance of 1.0. Other model parameters, all of which were assumed to be constant over time, were estimated using maximum likelihood. For the KF-RW model, the other parameters estimated were b, σ_v, and σ_w. For the KF-AR(1) model, we also estimated ϕ and $\bar{a}$. We formulated this analysis in S-Plus software (Venables and Ripley 1999). For more details on the Kalman filter method, also see Meinhold and Singpurwalla (1983), Harvey (1989), and Zeng et al. (1998).

For each stock, application of the Kalman filter to historical data on recruits and spawners resulted in a complete time series of annual a_t estimates from brood years 1956 through 1995. These are referred to as the "filtered" estimates (Harvey 1989), where each a_t estimate depends only on data up through year t. To derive the best estimates of historical productivity for each stock, we then produced "smoothed" estimates of a_t (Visser and Molenaar 1988). As detailed in Appendix A, the smoothed estimates were based on information provided by the entire time series of filtered a_t estimates. The smoothing approach worked backwards through time starting with the final brood year of the data series. The smoothed values of a_t are the minimum-variance unbiased estimates of a_t, as well as the maximum likelihood estimates (Fraser and Potter 1969). We emphasize that this procedure is *not* the same as simply applying a LOWESS or other common smoother. Instead, the smoothed Kalman filter estimates were derived from a quite different procedure in which the variance of each annual a_t estimate was used in a weighted calculation to obtain a_{t-1} (see Appendix A). Confidence intervals for the smoothed a_t series were derived from the smoothed posterior variance for a_t each year (Visser and Molenaar 1988).

To examine the degree of coherence in trends in productivity among stocks, we calculated Pearson product–moment correlation coefficients for pairwise comparisons between time series of reconstructed a_t values (or, in the case of the standard Ricker model, between time series of u_t). Data series for all comparisons were aligned by brood year.

In addition, we estimated autocorrelation functions for each time series of a_t (or u_t) estimates to examine the persistence of trends in productivity. From a practical management point of view, estimates of a_t should ideally be positively correlated with those in years $t + 6$ or $t + 7$. This is because for these stocks, about 84% of the fish mature by age 5 and 97% by age 6 years. Thus, parameter estimates for brood year t can only be obtained in year $t + 6$ after the 6-year-olds return as adult recruits (or in year $t + 5$ if one is willing to ignore a relatively small group of age-6 recruits). Any resulting change to management actions would then be applied in the following year at the earliest. Thus, for these stocks, managers can only take action based on revised parameter estimates 6 or 7 years after the brood year that experienced the change in productivity. Such actions will clearly be most appropriate if altered parameter values persist for that long. Autocorrelations of the a_t series estimate this persistence.

Time-varying optimal escapements and harvest rates

As shown below, the reconstructed Ricker a parameter for several stocks showed considerable temporal variation. We therefore estimated how optimal escapement (i.e., spawner abundance) changed over time. We used the entire data set to reconstruct the smoothed a_t values, as described above, and asked, knowing what we know now, what were the optimal escapements each year in the past if productivity changed as estimated? The Alaska Department of Fish and Game estimates optimal escapement as the abundance of spawners that produces maximum sustainable yield (MSY). This optimal escapement is a function of the a and b parameters. For the standard Ricker model, we estimated a constant optimal escapement across all brood years using estimates of a and b. In contrast, for the two Kalman filter models, we computed annual estimates of optimal escapement using the smoothed a_t estimates and the estimate of b. For a given combination of a and b estimates, we iteratively searched for the spawner abundance (S^*) that maximized the difference between total recruits and spawners, where the expected value of total recruits was estimated by exponentiating eq. 3:

$$(6) \qquad R = S[\exp(a + bS + \sigma_v^2/2)]$$

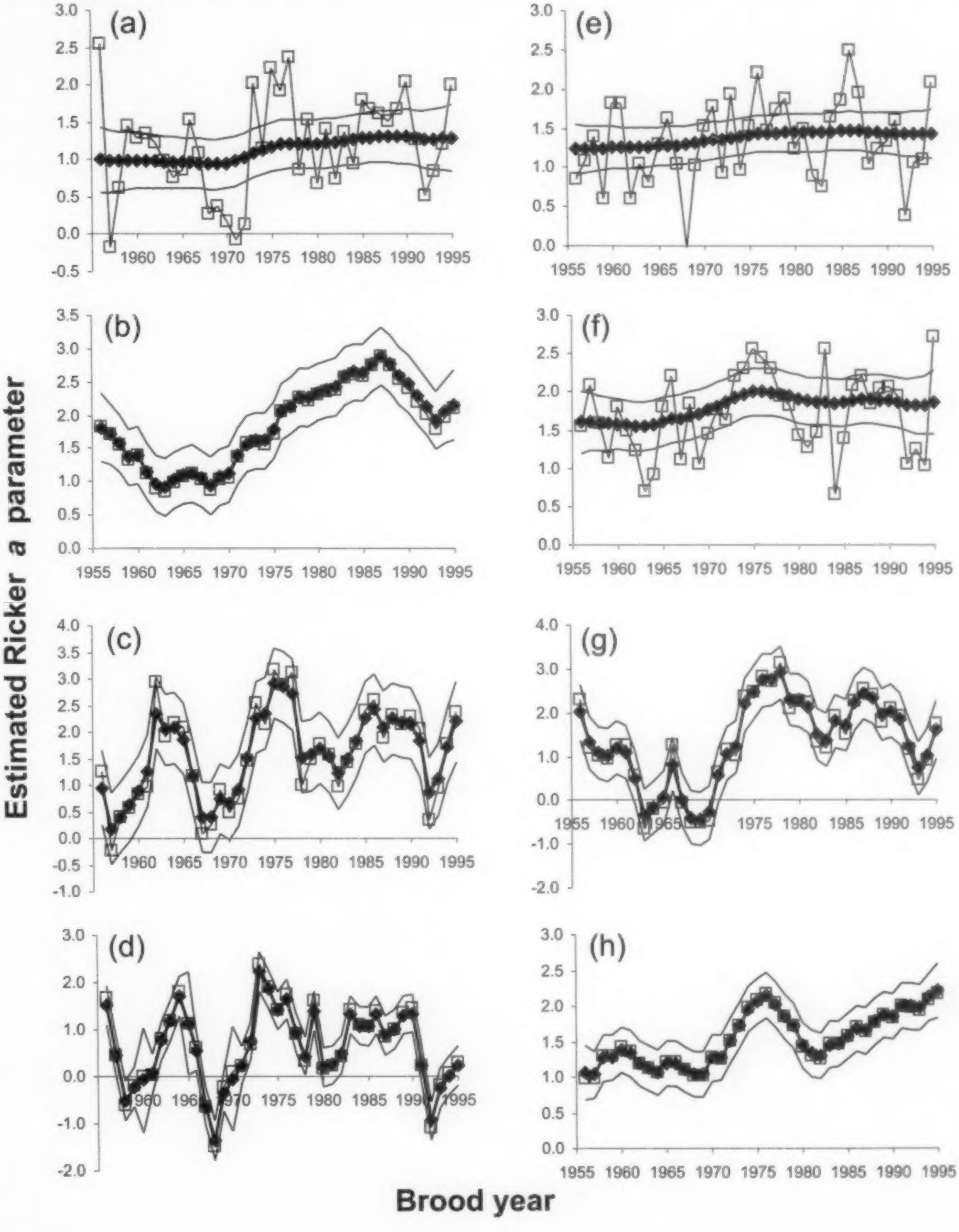
Adding $\sigma_v^2/2$ (or $\sigma_u^2/2$ for the standard Ricker model) to the exponent corrects for the bias incurred when back-transforming from the log-space of eq. 3 to eq. 6 (Hilborn and Walters 1992). The resulting optimal escapements (S^*) from the three models were compared with escapements that occurred historically.

Changes in productivity also affect the optimal proportion of recruits that should be harvested to meet a particular management objective. We estimated this optimal harvest rate as C^*/R^*, where R^* is the expected recruitment calculated from eq. 6 above using the optimal escapement, S^*, and the catch $C^* = R^* - S^*$. Again, we estimated a constant optimal harvest rate for the standard Ricker model, and annual (brood year specific) optimal harvest rates for the Kalman filter models. To compare these brood-year-specific harvest rates to historical harvest data (which are applied to several different brood classes of different ages in a given calendar year), we lined up the brood year optimal harvest rates with the actual harvest rates observed 5 years later. This is because the mean age at maturity of Bristol Bay sockeye salmon stocks is generally between 4.5 and 5 years. For the Kvichak and Ugashik stocks, it was not possible to estimate either S^* or optimal harvest rate for the few years in which smoothed a_t estimates were negative.

Results

All eight Bristol Bay sockeye salmon stocks showed evidence of trends in productivity as reflected by the time series of smoothed a_t estimates from the KF-RW and KF-AR(1) models (Fig. 1). However, most of our discussions will focus

Fig. 1. Smoothed a_t estimates from the Kalman filter AR(1) model (KF-AR(1); □) and from the Kalman filter random-walk model (KF-RW; ◆) by brood year. Thin solid lines indicate 95% confidence limits for a_t estimates from the KF-RW model. Results are for the major sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (*a*) Branch, (*b*) Egegik, (*c*) Igushik, (*d*) Kvichak, (*e*) Naknek, (*f*) Togiak, (*g*) Ugashik, and (*h*) Wood.



on results for the KF-RW model because it was deemed the most appropriate model for identifying long-term temporal trends in productivity for the following reasons.

The KF-AR(1) model did not add to our understanding of temporal trends in productivity. Its results were either identical to those from the standard Ricker model or very similar to the results from the KF-RW model. For four stocks — those with the lowest estimates of ϕ (Branch, Kvichak, Naknek, and Togiak) — the KF-AR(1) model gave a maximum likelihood estimate of zero for σ_v, the error in the observation equation (Table 1). This means that the KF-AR(1) model reduced to (i.e., produced the same parameter estimates as) the standard Ricker model (Table 1). Thus, for these four stocks, the KF-AR(1)-smoothed a_t estimates were equivalent to the residual errors from the standard Ricker model (those added to the estimate of the a parameter, i.e., $a + u_t$ from eq. 1). This resulted in highly variable time series of KF-AR(1)-smoothed a_t estimates, in particular for the Branch, Naknek, and Togiak stocks (Figs. 1*a*, 1*e*, and 1*f*). Such rapidly changing time series do not provide an appropriate basis for managers to alter escapement goals or harvest rates because they could end up "chasing noise" rather than an underlying varying signal reflecting changing mean productivity. In contrast, for the four stocks with larger ϕ estimates and nonzero σ_v estimates (Table 1; Egegik, Igushik, Ugashik, and Wood), the KF-AR(1) model produced a_t series almost identical to those of the KF-RW model (Figs. 1*b*, 1*c*, 1g, and 1*h*). The KF-RW model, on the other hand, produced smoothed a_t estimates for all eight stocks that exhibit trends on time scales that may be useful to fisheries managers (Fig. 1), i.e., patterns in productivity that do not vary as widely from year to year as residuals from the standard Ricker model. The remaining sections therefore emphasize results from the KF-RW model and are partly organized as answers to the five questions about trends in productivity that were posed in the Introduction.

What are the characteristics of the trends in productivity?

Some examples of time series of KF-RW smoothed a_t estimates illustrate the characteristics of trends in productivity. Smoothed a_t estimates for the Egegik stock increased from about 0.85 in brood year 1968 to about 2.8 in brood year 1987 (Fig. 1*b*). Recall that the a parameter is the expected value of the $\log_e$(recruits/spawner) at low spawner abundance, i.e., when there is little density dependence. Thus, the above change in a_t for the Egegik stock over the 20-year period represents about a sevenfold increase in median productivity at low spawner abundance ($\exp(a_t)$) from about 2.3 to 17 recruits/spawner. Although productivity of the Egegik stock increased, the Kvichak stock, which has historically been the most abundant sockeye salmon stock in the world, suffered about an 87% reduction in productivity from the 1973 to the 1995 brood years as estimated by the decrease in recruits per spawner at low abundance from ~9.3 to ~1.25 (Fig. 1*d*). (This series of a_t values for the Kvichak stock was not strongly influenced by the omission of the three data points; the correlation between this series and the a_t series that was reconstructed using all of the data was 0.95.) Some of the other stocks (e.g., Branch) showed a general increasing trend in mean productivity over the 40-year period. These and other such changes over time in productivity have important implications for sustainable harvest rates and escapement goals, as discussed below.

For some stocks, the KF-RW model attributed much more of the observed change in $\log_e(R/S)$ to error in the observation equation (σ_v in eq. 3) than to system-equation error (σ_w in eq. 4). For example, for the Branch, Naknek, and Togiak stocks, σ_v was between 0.5 and 0.63, compared with σ_w between 0.05 and 0.09 (Table 1). The relative magnitude of those sources of error is called the signal-to-noise ratio, i.e., σ_w^2/σ_v^2 (Chatfield 1989), which is very small in these three cases (≤ 0.04). For the other five stocks, the KF-RW model estimated that the observation-equation error was about of the same order as, or smaller than, the system-equation error (Table 1), and the signal-to-noise ratio was at least 11 times greater than for the Branch, Naknek, and Togiak stocks. This is reflected by the greater variation over time in the a_t values reconstructed by the KF-RW model for those five stocks (Figs. 1*b*, 1*c*, 1*d*, 1g, and 1*h*) compared with the other three stocks.

The stocks differed considerably in the persistence of the changes in a_t values, as reflected by the autocorrelations at various lags. Four stocks (Branch, Egegik, Naknek, and Togiak) had moderately large autocorrelations at lag 6 and 7 years (ranging from 0.48 to 0.63 at 6 years and 0.36 to 0.54 at 7 years). The Ugashik and Wood stocks had small positive autocorrelations at those lags (0 to 0.17), and the Igushik and Kvichak were negatively autocorrelated (–0.19 to –0.43).

The filtered estimates of a_t (Fig. 2, ○), i.e., those derived annually by the KF-RW model, were quite similar to the smoothed KF-RW estimates of a_t (Fig. 1), which were derived by the Kalman filter working backwards after all annual estimates of a_t were made for the entire data set. Across brood years 1957–1995, the pairwise correlations between these two series for each stock ranged from 0.76 for Branch to 0.99 for Ugashik, with a median r of 0.97 and mean of 0.88.

Are the trends shared among the stocks?

The extent to which the eight stocks of Bristol Bay sockeye salmon encounter similar environmental conditions should be reflected in the correlations among their temporal patterns in productivity. Correlations among the KF-RW smoothed a_t estimates for different stocks indicate that changes in productivity were widely shared among those stocks (Fig. 3*b*). These smoothed estimates of a_t tended to show greater positive covariation in productivity among the eight stocks than previously (Peterman et al. 1998) indicated by simply examining correlations among residuals in $\log_e(R/S)$ from the standard Ricker model (i.e., u_t from eq. 1). The median of the 28 pairwise correlations among the eight time series of KF-RW smoothed a_t estimates (Fig. 3*b*) was 0.65 (mean = 0.6), compared with the median of correlations among the u_t residuals of 0.43 (mean = 0.43) for the standard Ricker model (Fig. 3*a*).

This shared variation among stocks is even more evident when time series of a_t (Fig. 1) or u_t are standardized (mean of zero, standard deviation of 1) and superimposed on one graph (Fig. 4). Standardized estimates from both the standard Ricker model (Fig. 4*a*) and the KF-RW model (Fig. 4*b*) indicate a common tendency among all eight stocks to show

Table 1. Optimal parameter values estimated by maximum likelihood for each of the Bristol Bay sockeye salmon stocks for the constant parameters of the two forms of the Kalman filter, a random-walk model (eqs. 2 and 3) and an autoregressive (AR(1)) model (eqs. 2 and 4).

	Branch	Egegik	Igushik	Kvichak	Naknek	Togiak	Ugashik	Wood
Kalman filter random-walk (RW) model								
σ_v	0.63 (0.08)	0.38 (0.06)	0.43 (0.16)	0.22 (0.37)	0.51 (0.06)	0.50 (0.07)	0.38 (0.15)	0.26 (0.05)
σ_w	0.08 (0.09)	0.25 (0.08)	0.62 (0.17)	0.74 (0.20)	0.05 (0.05)	0.09 (0.10)	0.58 (0.15)	0.21 (0.06)
σ_w^2/σ_v^2	0.02	0.42	2.04	11.6	0.01	0.04	2.27	0.64
b	–1.568 (0.51)	–0.305 (0.20)	–1.773 (0.41)	–0.022 (0.03)	–0.320 (0.14)	–4.294 (1.13)	–0.453 (0.16)	–0.617 (0.11)
Log-likelihood	–4.18	5.91	–12.61	–10.87	3.85	3.79	–8.87	17.75
Kalman filter AR(1) model								
σ_v	0.00 (0.43)	0.37 (0.07)	0.17 (0.66)	0.00 (0.21)	0.00 (0.82)	0.00 (0.87)	0.23 (0.32)	0.25 (0.05)
σ_w	0.61 (0.07)	0.27 (0.09)	0.74 (0.22)	0.71 (0.08)	0.52 (0.06)	0.51 (0.06)	0.67 (0.18)	0.22 (0.06)
Mean a	1.155 (0.17)	1.883 (0.58)	1.623 (0.32)	0.568 (0.29)	1.350 (0.19)	1.714 (0.20)	1.265 (0.46)	1.709 (0.30)
b	–1.844 (0.50)	–0.271 (0.20)	–1.746 (0.41)	–0.026 (0.03)	–0.289 (0.13)	–3.752 (0.98)	–0.432 (0.16)	–0.614 (0.11)
ϕ	0.24 (0.15)	0.91(0.09)	0.58 (0.20)	0.56 (0.13)	0.17 (0.16)	0.25 (0.17)	0.76 (0.14)	0.84 (0.12)
Log-likelihood	–0.33	6.67	–8.90	–5.90	6.33	6.44	–6.69	19.39
Standard Ricker model (with an AR(1) error term)								
σ_ε	0.61 (0.07)	0.54 (0.06)	0.76 (0.09)	0.71 (0.08)	0.52 (0.06)	0.51 (0.06)	0.72 (0.08)	0.39 (0.04)
a	1.155 (0.17)	1.684 (0.35)	1.618 (0.31)	0.568 (0.29)	1.350 (0.19)	1.714 (0.20)	1.270 (0.44)	1.605 (0.21)
b	–1.844 (0.50)	–0.146 (0.21)	–1.746 (0.41)	–0.026 (0.03)	–0.289 (0.13)	–3.752 (0.98)	–0.436 (0.16)	–0.625 (0.12)
ϕ	0.24 (0.15)	0.68 (0.12)	0.56 (0.14)	0.56 (0.13)	0.17 (0.16)	0.25 (0.17)	0.72 (0.11)	0.59 (0.14)
Log-likelihood	–0.33	4.57	–8.91	–5.90	6.33	6.44	–6.76	17.19

Note: Standard errors (SE) of these parameter values are in parentheses. Analyses were based on data for abundances of recruits and spawners expressed in millions of fish. Optimal parameter estimates and their standard errors are also given for the standard Ricker model, which assumes an AR(1) error structure. σ_v is the standard deviation of the observation-equation error for eq. 3, σ_w is the standard deviation of the system-equation error for eqs. 4 and 5 for the Kalman filter random-walk and Kalman filter AR(1) models, respectively, and σ_w^2/σ_v^2 is the signal/noise ratio. σ_ε is the standard deviation of the error term for eq. 2 (the standard Ricker model). Other parameter estimates are for b, mean a, and ϕ (autocorrelation coefficient in eq. 5). Log-likelihood values are provided for each model.

Fig. 2. Filtered (○) and smoothed (◆) estimates of a_t derived by the Kalman filter random-walk (KF-RW) model, by brood year, for sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (*a*) Branch, (*b*) Egegik, (*c*) Igushik, (*d*) Kvichak, (*e*) Naknek, (*f*) Togiak, (*g*) Ugashik, and (*h*) Wood.

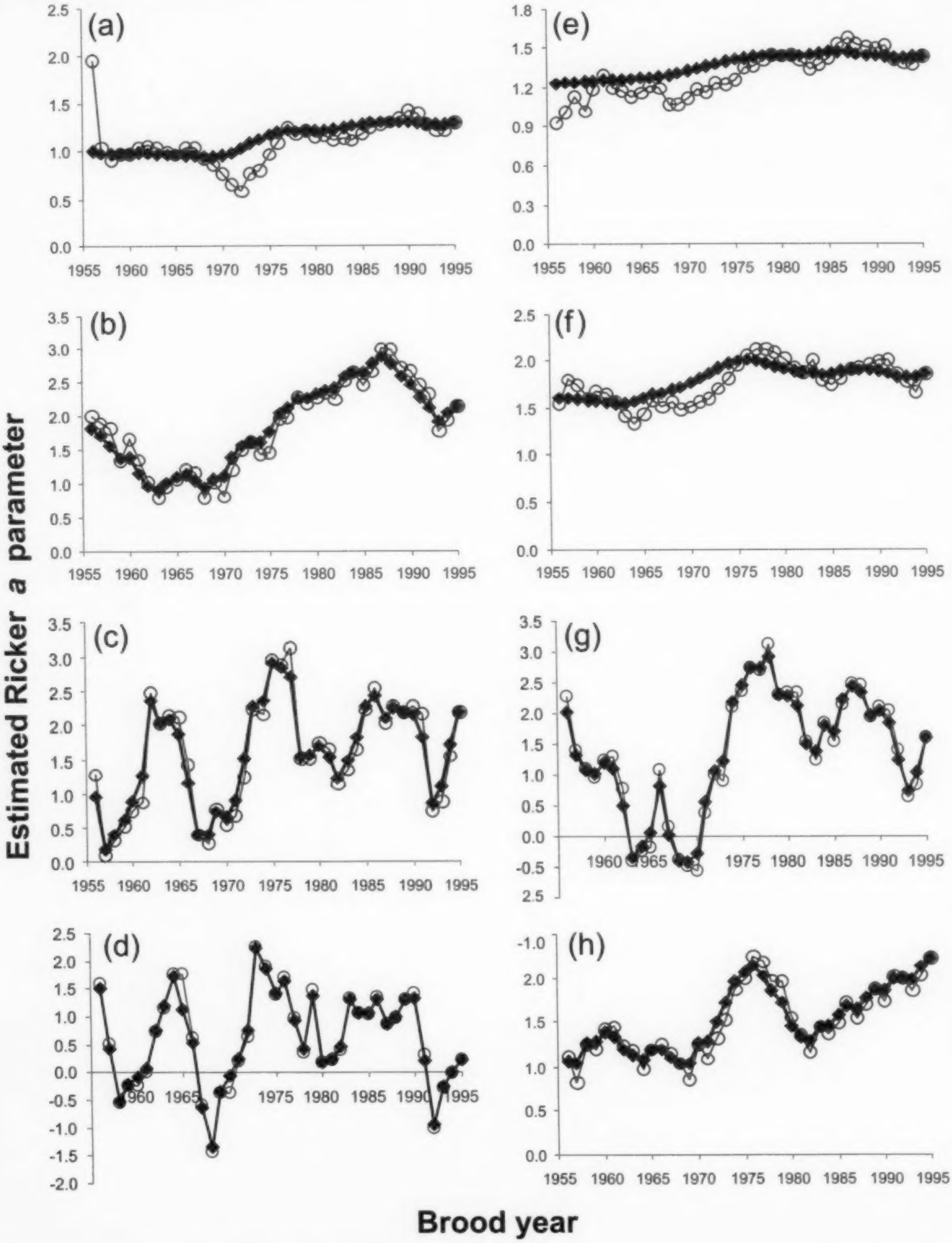
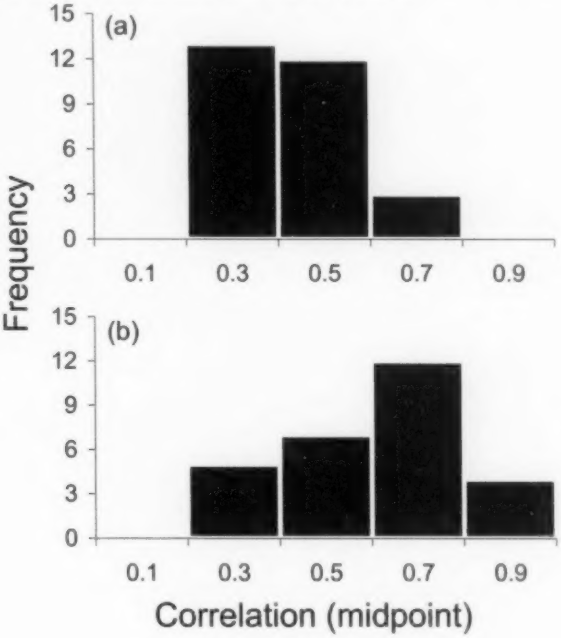


Fig. 3. Frequency distributions of the 28 correlations (*a*) among residuals from the standard Ricker model (u_t in eq. 1) in units of $\log_e$(recruits/spawner) and (*b*) among smoothed a_t estimates from the Kalman filter random-walk (KF-RW) model.



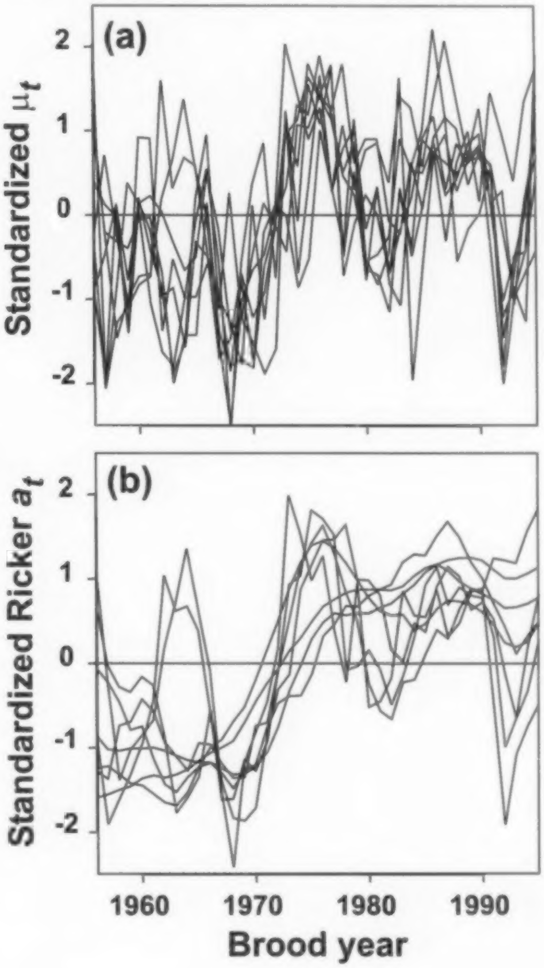
a rapid increase in productivity beginning in the late-1960s brood years. This tendency is particularly clear in the KF-RW results (Fig. 4*b*) because the Kalman filter attributed some of the high-frequency variation in the data to the variance in the observation equation ("noise", which likely includes random process error and measurement error), thus isolating more of the underlying trend ("signal") in mean productivity.

Some important differences among stocks also emerge from the standardized a_t values in Fig. 4*b*. Two stocks, the Igushik and Kvichak, were unusual in having relatively high *a* values in the 1960s brood years. More interestingly, starting with brood year 1990, the coherence among stocks observed since the late 1960s broke down to some extent as the trends in a_t diverged for different stocks (Fig. 4*b*). In this post-1990 period, the Kvichak stock had the largest negative deviations in *a* values from the long-term mean, whereas the Wood stock had the largest positive deviations.

What are the implications of trends in productivity for optimal escapements and harvest rates?

The changes in a_t exhibited by the Bristol Bay sockeye salmon stocks, especially the relatively rapid changes within 10-year periods in the Igushik, Kvichak, and Ugashik stocks (Figs. 1*c*, 1*d*, and 1*g*), are important to management. The a_t values for the Igushik and Ugashik stocks, for instance, both increased over a range of about three over an 8-year period starting with brood year 1969 and decreased by about one-third to one-half of that over the next 7 years. Because optimal management regulations are a function of the parameter values of the Ricker model (Ricker 1975), such strong time trends in productivity suggest that in such situations, appropriate harvest rates and escapement goals should be revised appreciably and in a timely manner, more so than would be the case when management advice is based on a standard (i.e., constant-parameter) Ricker model.

Fig. 4. Standardized time series for all eight Bristol Bay sockeye salmon (*Oncorhynchus nerka*) stocks of (*a*) residuals from the standard Ricker model (u_t in eq. 1) and (*b*) smoothed a_t estimates from the Kalman filter random-walk (KF-RW) model. Time series were standardized to have a mean of zero and a standard deviation of 1.



For instance, optimal escapements (defined as those producing MSY) based on the a_t values reconstructed by the KF-RW model changed annually and in some years differed considerably from the optimal values estimated by the standard Ricker model (Fig. 5). Brood years in which KF-RW estimates of a_t increased (Fig. 1) were associated with increases in estimates of optimal escapement (Fig. 5). For some stocks, the KF-RW estimates of optimal escapement were greater than the actual escapements in most years (e.g., Branch, Egegik, and Naknek), whereas in other stocks, the

Fig. 5. Actual spawner abundances (solid line) and optimal spawner abundances (◆ for the Kalman filter random-walk (KF-RW) model; broken line for the standard Ricker model) by brood year for 1956–1995. Four data points were off-scale for actual spawner abundances, three for Branch in 1956 (0.78 million fish), 1959 (0.83), and 1960 (1.24), and one for Igushik in 1980 (1.99). The broken line for the Egegik is off-scale at 4.4 million fish. Results are for sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (*a*) Branch, (*b*) Egegik, (*c*) Igushik, (*d*) Kvichak, (*e*) Naknek, (*f*) Togiak, (*g*) Ugashik, and (*h*) Wood.

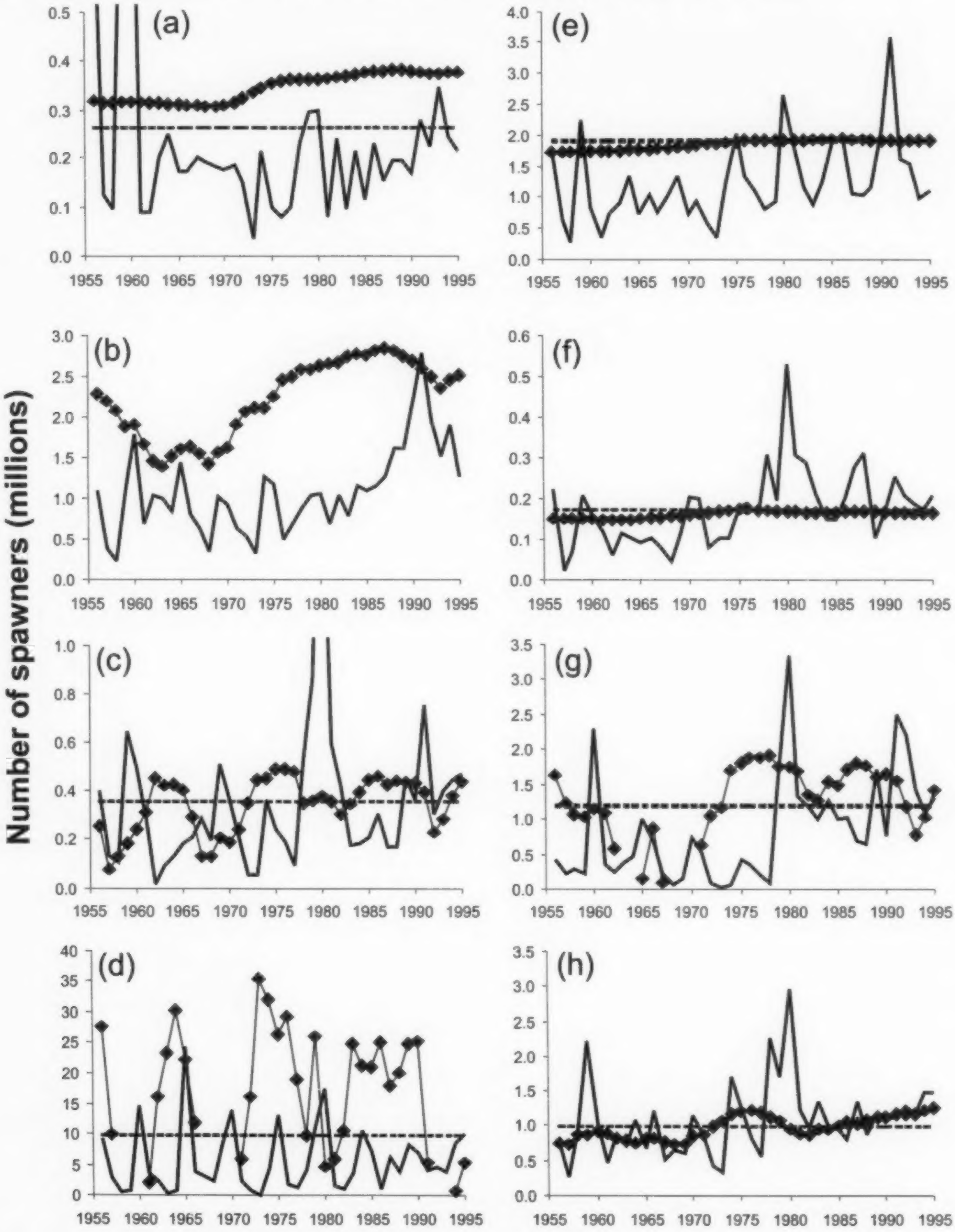
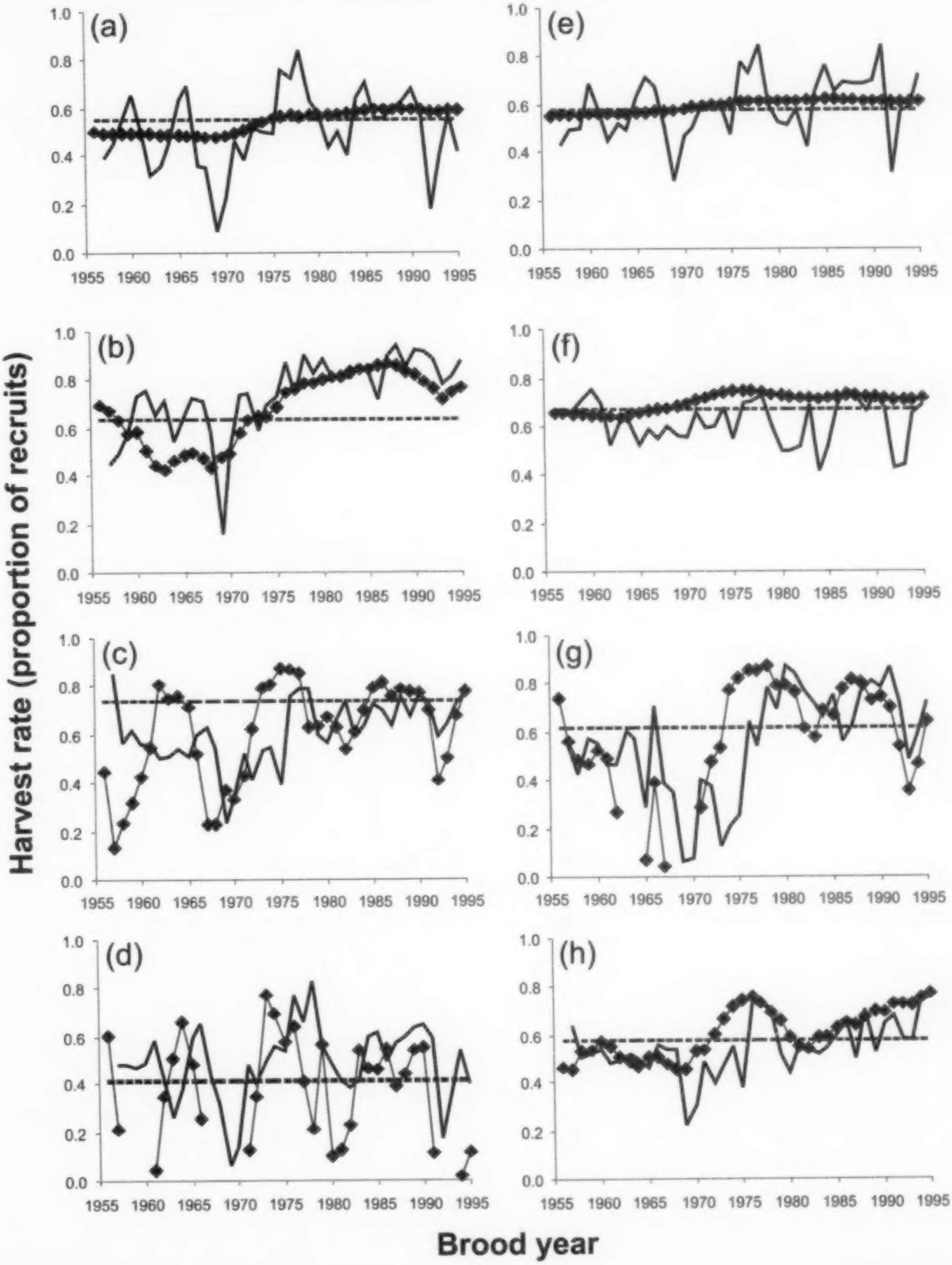


Fig. 6. Optimal harvest rates (proportion of recruits) for the standard Ricker model (broken line) and the Kalman filter random-walk (KF-RW) model (◆), by brood year *t*. Estimates for the Ricker model were based on single *a*, *b*, and σ_u^2 parameter values for each stock, whereas optimal harvest rate estimates for the KF-RW model were based on the reconstructed time-varying a_t values and the fixed *b* and σ_v^2 estimates. Actual proportional harvest rates (solid line) that occurred in calendar year *t* + 5 are plotted at brood year *t*, reflecting a 5-year age-at-maturity. Results are for sockeye salmon (*Oncorhynchus nerka*) stocks in Bristol Bay, Alaska: (*a*) Branch, (*b*) Egegik, (*c*) Igushik, (*d*) Kvichak, (*e*) Naknek, (*f*) Togiak, (*g*) Ugashik, and (*h*) Wood.



estimated and actual escapements were in a similar range (Fig. 5).

Optimal proportional harvest rates estimated by the KF-RW model were generally in similar ranges to both the actual historical harvest rates and the optimal rates derived from the standard Ricker model (Fig. 6). However, as with optimal escapements, there were periods when these rates differed considerably. For instance, in the late-1960s brood years when a_t values tended to be relatively low (Fig. 1), the KF-RW estimates of optimal harvest rate were much lower than the standard Ricker model estimates (e.g., Figs. 6*b*, 6*c*, 6g, Egegik, Igushik, and Ugashik, respectively). When a_t values were high in the 1970s brood years for most stocks, optimal exploitation rates from the KF-RW model tended to be higher (by between 0.01 and 0.36) than suggested by the standard Ricker model and higher (by between 0.08 and 0.4) than actual harvest rates (e.g., Togiak, Igushik, Ugashik, and Wood) (Fig. 6). In other stocks, all three harvest rates were quite comparable during that period of increasing productivity.

Discussion

The reconstructions from the Kalman filter random-walk (KF-RW) model showed strong evidence of temporal changes in productivity of the eight Bristol Bay sockeye salmon stocks. Many stocks showed a general tendency for increasing Ricker *a* parameters over time during the 40-year period, reflecting increased recruits produced per spawner at low abundance. Some stocks showed 5- to 28-fold increases in recruits per spawner at low spawner abundance over this period, but even stocks without such dramatic changes showed increased recruits per spawner (e.g., Naknek, 27% increase; Branch, 45%).

However, the nature of these trends varied qualitatively among certain groups of stocks. Specifically, the Igushik, Kvichak, and Ugashik stocks showed wide-ranging increasing and decreasing trends over a decade or less, whereas the Egegik and Wood stocks showed fairly steady but less-rapid large changes over two or more decades. The latter decadal-scale changes are consistent with Finney et al'.s (2000) conclusion that Karluk Lake sockeye salmon vary over multi-decadal scales (Karluk Lake is on the south side of the Alaskan peninsula from Bristol Bay), if those variations were due to changes in productivity. Our time trends in productivity also show examples that are qualitatively consistent with Ware's (1995) three dominant periodic components of physical oceanographic and atmospheric variables (5–7, 25, and 50 years).

Although it is clear that the point estimates of a_t from the Kalman filter random-walk model show important changes through time for most stocks, the confidence intervals on those estimates are too small. This is because the confidence limits are conditional on the maximum likelihood estimates of the constant parameters in Table 1. If full uncertainty in those parameters were accounted for, the confidence intervals would be wider.

Management implications

Some stocks showed large changes over time in optimal escapement as estimated by the KF-RW model, and these estimates often differed considerably from optimal escapements estimated by the normal approach, i.e., a standard Ricker model. These differences have important management implications. They suggest that using a Kalman filter approach that assumes some form of time-varying parameter may lead to different escapement goals and perhaps greater long-term benefits, as demonstrated by the simulation results of Peterman et al. (2000).

A comparison of actual escapements with optimal escapements derived from the Kalman filter model shows that in some stocks such as the Wood stock, actual escapements were near the optimal values and had similar temporal trends. However, in other cases, actual escapements were consistently lower than optimal values (Branch, Egegik, and Naknek). Note that actual escapements reflect not only the escapement goals of the management agency, but also differences between desired and target escapements caused by inherent difficulties of in-season estimation of run sizes and management of fishing effort.

From the viewpoints of conservation and economic benefits, the proportion of recruits harvested should go down when stocks become less productive and increase when they become more productive. The KF-RW optimal harvest rate estimates do this because of the constant *b* parameter and time-varying *a* values. Actual historical harvest rates also tended to change in the correct direction as a_t values changed, although often with a several-year lag behind the optimal ones estimated by the KF-RW model (Igushik, Kvichak, Ugashik, and Wood stocks). In addition, actual proportional harvest rates tended to vary more widely than the KF-RW optimal values (lower than needed or higher than advisable). Thus, costs were incurred through foregone present or future catches. These results suggest that there are advantages to using models with time-varying parameters, which can help reduce risks when populations become relatively unproductive and take advantage of increased productivity.

Generally, the actual and estimated optimal harvest rates were in closer agreement than were the actual and estimated optimal spawner abundances. This difference largely reflects the fact that the optimal proportional harvest rate for a goal of MSY is only a function of the Ricker *a* parameter, whereas the optimal spawner abundance is a function of both Ricker *a* and Ricker *b* parameters. The *b* parameter for a given stock is often imprecisely estimated because of a lack of good contrast in the data, few data points at high abundance, and large variability. Our results indicate that despite the constant escapement policy used by the Alaska Department of Fish and Game, actual proportional harvest rates were historically closer to the optimal harvest rates estimated by the KF-RW than actual escapements were to optimal escapements. This suggests that proportional harvest-rate targets might be more reliably estimated and easier to achieve.

The difficulty of recognizing changes in underlying mean productivity of salmon in a timely manner amid highly variable data suggests that salmon scientists and managers need more sophisticated models, such as the Kalman filter. This need is particularly acute in the presence of climatic change. Although climate is likely to alter salmon productivity, there is considerable uncertainty about the direction and rate of change in productivity on the west coast of North America (Beamish 1995). Models with time-varying parameters should also improve estimates of temporally trended but uncertain effects of human activities and natural processes on freshwater habitat for salmon (e.g., destruction of spawning or rearing habitat through erosion or sedimentation).

Although we have shown that the KF-RW model has advantages over standard methods for several Bristol Bay sockeye salmon stocks, this advantage will likely be smaller for the four stocks that exhibit little positive temporal autocorrelation in productivity (e.g., Igushik, Kvichak, Ugashik, and Naknek). For example, such low autocorrelation at a lag of 6 or 7 years will reduce the benefits of the KF-RW model as a tool for setting escapement goals because the productivity estimated in a given year may no longer be applicable a generation later. As well, British Columbia sockeye salmon south of the Skeena River and most Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*) stocks show low autocorrelation in the past (Korman et al. 1995; Peterman et al. 1998; Pyper et al. 2001). However, future temporal trends in productivity may be different if climatic changes continue. In that event, it is worth considering the use of models that assume time-varying parameters to detect such changes in a timely manner.

Biological interpretation

The causes of the changes in productivity of a given Bristol Bay sockeye stock are not clear. Previous analyses of spawner-to-recruit survival rate indices for these stocks suggest that they vary as a result of changes in both marine and freshwater survival rates, with marine conditions generally being the larger contributor to changes (Peterman et al. 1998), but other possibilities exist. For example, the eight Bristol Bay stocks examined here are composed of large numbers of relatively independent spawning groups (substocks; e.g., there are 93 known unique spawning areas thought to represent substocks in one of the two lakes in the Kvichak system (Iliamna); Michael Link, LGL Ltd., 9768 Second Street, Sidney, BC V8L 3Y8, personal communication). It is possible that the magnitude and rate of change in the Ricker a parameter reported here for the Bristol Bay sockeye stocks is due to a change in the substock composition of the stock group in which the relative contribution of the more productive substock(s) either increased or decreased (Michael Bradford, Canada Department of Fisheries and Oceans and the Cooperative Resource Management Institute at Simon Fraser University, Burnaby, BC V5A 1S6, personal communication). For instance, differential harvesting of these substocks based on their different timing of adult returns is one mechanism that could cause such a change. However, this mechanism seems unlikely because the change in smoothed a_t values was both rapid and reversed direction several times in many of the stocks. It is also unlikely that the observed changes were due to alteration in the quality of spawning and rearing habitat, either for specific substocks or overall; habitat in the region is relatively undisturbed by human activities. It is likely that some of the estimated variability in a_t values from year to year is due to different levels of interception of a given stock in other fishing districts. However, such measurement error is not likely the source of temporal trends (slowly changing a_t values) unless there was a systematic change over time in bias of sampling, aging, stock identification, etc. Such trends in bias seem unlikely.

Do trends in productivity correspond with the mid-1970s regime shift?

In general, the reconstructed estimates of a_t demonstrate rapid increases in productivity across stocks about the time of the so-called "regime shift" in the mid-1970s. For a given brood year t, most Bristol Bay sockeye salmon juveniles migrate to the ocean in either year $t + 2$ or $t + 3$. Thus, the reconstructed estimates of a_t are generally consistent with the best-fit models of Adkison et al. (1996) and Peterman et al. (1998), which suggested that higher survival rates occurred starting with the 1973 brood year (i.e., 1975 ocean-entry year at the earliest).

However, our results also suggest that trends in productivity of Bristol Bay sockeye salmon showed greater complexity over time and diversity among stocks than indicated by the simple step functions used in previous analyses to describe the mid-1970s regime shift (e.g., Hare and Francis 1995; Adkison et al. 1996). For instance, as noted above, the Igushik, Kvichak, and Ugashik stocks experienced several coherent and wide-ranging fluctuations in productivity both before and after the mid-1970s, whereas the Egegik and Wood stocks showed fairly steady but less-rapid large changes over the 40-year period. Such diversity likely reflects the complexity of mechanisms and processes by which physical and biological conditions influence the productivity of individual stocks — a complexity far greater than reflected by the simplistic concept of decadal-scale regime shifts.

Is there evidence of a recent regime shift?

Some researchers have found evidence for another regime shift in 1989 in various biological components of the Northeast Pacific ecosystem (Hare and Mantua 2000). We see little consistent evidence of this for Bristol Bay sockeye salmon. Although several stocks (e.g., Egegik, Igushik, Kvichak, and Ugashik) showed decreased smoothed a values beginning in the late 1980s, that decrease appears to have been short-lived rather than persistent. Our conclusions on this point may be weak because of the lack of complete brood years beyond 1995 (6-year-old fish just returned in 2001). Nevertheless, at present it appears too early to conclude that any regime shift in productivity of Bristol Bay sockeye salmon occurred in 1989 or later, despite evidence for such a shift across other biological components of the ecosystem.

In conclusion, the strong positive covariation among smoothed KF-RW estimates of a for the eight Bristol Bay sockeye stocks indicates that their productivities respond more similarly to environmental conditions than previously indicated by studies involving residuals of $\log_e$(recruits/spawner) (e.g., Peterman et al. 1998). The latter study was based on fitting the standard Ricker model under the assumption that its parameters are constant over time. In contrast, the Kalman filter attributed some of the observed variation in recruits/spawner to observation-equation error (random process error and measurement error), thus revealing a time series of reconstructed a values that reflect more of the systematic medium- to long-term trends in underlying ecological or process variation than has been possible previously. In this way, a Kalman filter is better able to estimate slowly changing underlying trends in productivity amid large interannual variation and measurement error than is a model with constant parameters. Stronger correlations among the eight Bristol Bay stocks thus emerged from the reconstructed estimates from the KF-RW model.

Not only do such reconstructed estimates of stock productivity provide insight into past changes in the ecological system, but they also may provide better dependent variables than previously available for studying the influence of environmental variables on fish productivity (Mueter et al. 2002). Future studies of potential relationships between salmon survival rates and environmental conditions should consider using smoothed Kalman filter estimates of productivity as shown here.

Finally, our reconstructed trends in past productivity of sockeye salmon stocks resulted from the random-walk version of a Kalman filter estimation procedure. For tracking simulated trends in productivity, this was the best method of the ones examined by Peterman et al. (2000). However, there are other methods for estimating trends in parameters, but to our knowledge, the performance of those methods has not yet been examined via simulations. For instance, models that assume both time-varying Ricker *a* and Ricker *b* parameters are possible, as are other forms of Box–Jenkins type time series models. It is conceivable that these other methods might estimate different temporal patterns in productivity.

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Appendix A. Kalman filter procedures

Overview

The Kalman filter is a recursive procedure for making inferences about the state of nature, in this case, a_t, based on observed data, $\log_e(R_t/S_t)$. To reconstruct values of a_t through time, the first step in applying the Kalman filter to the Ricker model (eqs. 3 through 5 above) is to determine the prior probability distribution for a_t. In the first year, we used a broad distribution (standard deviation (SD) = 1 with a mean of 1), whereas in subsequent years, equations determined the prior distribution for a_t. This prior distribution was used to predict $\log_e(R_t/S_t)$ one year into the future. Second, estimates for the mean and variance of a_t were updated based on how well the model predicted the next observation (Meinhold and Singpurwalla 1983). This procedure was applied iteratively, working through the data set one year at a time. We then applied a smoothing algorithm to these filtered estimates to obtain smoothed estimates of a_t, which take into account information from the entire data set (Harvey 1989). The procedures below are drawn from Meinhold and Singpurwalla (1983), Visser and Molenaar (1988), Chatfield (1989), and Peterman et al. (2000).

Prior distribution

The prior value (denoted by the subscript $t|t-1$ because it is the value at time t, given the information up to $t-1$) for the mean of a_t is a function of the posterior value from the previous year (denoted by the subscript $t-1|t-1$). The prior means for the random walk and AR(1) Kalman filter (KF-RW and KF-AR(1), respectively) models are given respectively by the system equations:

(A1) $a_{t|t-1} = a_{t-1|t-1}$

(A2) $a_{t|t-1} = \bar{a} + \phi(a_{t-1|t-1} - \bar{a})$

Similarly, the prior variance of a_t ($P_{t|t-1}$) depends on the posterior variance from the previous year ($P_{t-1|t-1}$). Prior variances for the random walk and AR(1) models, respectively, are given by

(A3) $P_{t|t-1} = P_{t-1|t-1} + \sigma_w^2$

(A4) $P_{t|t-1} = \phi^2 P_{t-1|t-1} + \sigma_w^2$

For the first year of data, no posterior estimates from the previous year were available, so initial guesses were used. We assumed an initial value of 1.0 for both the prior mean and prior variance of a_t for the first year (i.e., $a_{1|0} = P_{1|0} = 1$). These values were arbitrary, but it has been shown that estimates are updated quickly by the Kalman filter starting with these initial values so that subsequent estimates are soon dominated by the data (Chatfield 1989), especially with longer time series such as ours (Zeng et al. 1998).

Posterior distribution

The first stage for updating prior estimates of the mean and variance of a_t is the prediction stage (Chatfield 1989). The one-step-ahead prediction error (e_t) was calculated by predicting $\log_e(R_t/S_t)$ using the prior mean for a_t and subtracting this prediction from the observed value:

(A5) $e_t = \log_e(R_t/S_t) - (a_{t|t-1} + bS_t)$

The variance (f_t) of this prediction error is given by:

(A6) $f_t = P_{t|t-1} + \sigma_v^2$

These values were then used in the updating equations to derive the filtered (i.e., posterior) estimates of the mean ($a_{t|t}$) and variance ($P_{t|t}$) of a_t:

(A7) $a_{t|t} = a_{t|t-1} + \dfrac{P_{t|t-1}e_t}{f_t}$

(A8) $P_{t|t} = P_{t|t-1} - \dfrac{P_{t|t-1}^2}{f_t}$

For the 3 years of omitted data for the Kvichak stock, the posterior values for the mean and variance of a_t were set to equal the prior values (i.e., $a_{t|t} = a_{t|t-1}$ and $P_{t|t} = P_{t|t-1}$) and the updating eqs. A5–A8 were omitted (e.g., Zeng et al. 1998). This is essentially equivalent to assuming that the omitted data points have infinite observation–equation variances (σ_v^2).

Maximum likelihood estimates of constant parameters

Iteratively applying eqs. A1 through A8 produced a time series of filtered estimates ($a_{t|t}$) that was conditional on estimates of the other constant parameters. Estimates of these constant parameters (b, σ_v, and σ_w in the KF-RW model or b, ϕ, $\bar{a}$, σ_v, and σ_w in the KF-AR(1) model) were obtained by maximizing the following "concentrated" likelihood function over the entire data set (Harvey 1989):

(A9) $\log_e(L_c) = -\dfrac{1}{2}\left[\sum_{t=2}^{N}\log_e(f_t) + \sum_{t=2}^{N}\dfrac{e_t^2}{f_t}\right]$

where N is the total number of years of data. As in Zeng et al. (1998), we conditioned our estimates on the first year of data to limit the influence of the initial, arbitrary prior distribution. Standard errors of these constant parameters were estimated via the information matrix, i.e., the second partial derivatives of the log-likelihood function (Pella 1993).

Smoothed estimates

The filtered estimates provide the expected value of a_t conditional on all information through time t, but they do not take account of information after time t. The object of Kalman filter smoothing is to produce better estimates of the a parameter (denoted with the subscript $t|N$) that are conditional on information from the entire data set (Harvey 1989). The smoothed estimates have a mean-squared error less than (or equal to) that of the filtered estimates. Note that in the final year ($t = N$), the smoothed estimates of the mean and variance of a_t are equal to the filtered estimates for that year. For the remaining years, the smoothing procedure works backwards from $t = N - 1$ to $t = 1$. This is known as "fixed-interval smoothing", and the resulting smoothed estimate at a given time t is a weighted average of the smoothed estimate at time $t + 1$ and the filtered estimate at time t (Harvey 1989). The smoothed estimates of the mean and variance of a_t, respectively, are given by

$$\text{(A10)} \quad a_{t|N} = a_{t|t} + P_t^*(a_{t+1|N} - a_{t+1|t})$$

$$\text{(A11)} \quad P_{t|N} = P_{t|t} + (P_t^*)^2(P_{t+1|N} - P_{t+1|t})$$

where values of P_t^* for the KF-RW and KF-AR(1) models, respectively, are given by

$$\text{(A12)} \quad P_t^* = \frac{P_{t|t}}{P_{t+1|t}}$$

$$\text{(A13)} \quad P_t^* = \phi \frac{P_{t|t}}{P_{t+1|t}}$$

Unlike the filtered estimates, smoothing greatly reduces the influence of starting values for the prior distribution of a_t used to initialize the Kalman filter (Visser and Molenaar 1988).

Digestion of pelagic Ctenophora and Cnidaria by fish

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Abstract: The diet of chum salmon (*Oncorhynchus keta*) can range from a primarily arthropod to a primarily gelatinous composition. Because no data exist for the digestion rates of gelatinous prey in any fish, it has not been possible to convert data on stomach contents to feeding rates. We measured rates of digestion to address this issue. In freely feeding age-0 chum salmon, the ctenophore *Pleurobrachia bachei* was digested almost completely within 1 h, whereas 70% of shrimp sections of similar mass remained after 5 h at 13°C. To examine the fast progress of digestion at smaller intervals, age-0 and age-1 fish were also force-fed with whole *P. bachei* or sections of the hydromedusa *Aequorea victoria*. These data emphasize the necessity of examining fish stomachs very quickly after capture. Although gelatinous organisms have high water and salt content relative to their organic content, given the rapid rates of digestion observed, coelenterates might rival arthropods as energy sources.

Résumé : Le régime alimentaire du saumon kéta (*Oncorhynchus keta*) peut varier d'une dominance d'arthropodes à une dominance de matière gélatineuse. Puisqu'il n'existe pas de données sur les taux de digestion des proies gélatineuses chez les poissons, il n'est pas possible de convertir les données provenant de l'analyse des contenus stomacaux en taux d'alimentation. Nous avons donc mesuré des taux de digestion pour résoudre ce problème. Chez des saumons d'âge 0 se nourrissant à volonté, le cténophore *Pseudobrachia bachei* est presque complètement digéré en moins de 1 h, alors que 70 % des tranches de crevettes de même masse sont encore présentes après 5 h à 13°C. Pour examiner le déroulement rapide de la digestion à des intervalles de temps plus courts, nous avons alimenté de force des poissons d'âges 0 et 1 de *P. bachei* entiers ou de sections de l'hydroméduse *Aequorea victoria*. Ces résultats font valoir la nécessité d'examiner les estomacs de poissons très rapidement après la capture. Bien que les organismes gélatineux aient de forts contenus en eau et en sels comparativement à leur contenu organique, les coelentérés peuvent s'avérer aussi importants que les arthropodes comme sources d'énergie, compte tenu de la vitesse à laquelle ils sont digérés.

[Traduit par la Rédaction]

Introduction

Examination of stomach contents shows that gelatinous organisms form a portion of the diet of a wide variety of fish species, including such common and commercially important species as butterfish (*Peprilus* spp.), spiny dogfish (*Squalus acanthias*), chum salmon (*Oncorhynchus keta*), sablefish (*Anoplopoma fimbria*), and representatives of the Gadidae, Scorpaenidae, and Scombridae (Arai 1988; Brodeur and Pearcy 1992; Purcell and Arai 2001). Digestion of gelatinous prey was expected to be very fast as Jackson et al. (1987) showed that mammalian pepsin digested pieces of a scyphozoan medusa approximately 50 times faster than a comparable mass of crustacean muscle. Nevertheless, because there were no quantitative data on the passage times of gelatinous prey through fish digestive tracts, it has not been possible to convert data on stomach contents to feeding rates and hence to calculate the relative value of this prey to the diets. The present study examined the rates at which one fish species, chum salmon, digests ctenophores and hydromedusae.

As shown in a number of studies, *O. keta* prey on gelatinous taxa more commonly and in greater quantities than do the other salmon species The diets of field-caught chum salmon vary from primarily arthropod to primarily gelatinous composition depending on age, season, year, and locality (Tadokoro et al. 1996; Ishida et al. 1997; Davis et al. 1998). Coelenterate prey have rarely been reported in chum diets in their first weeks in salt water. In late summer as the fish increase in size and start to migrate, they begin to feed on different and larger prey, including ctenophores (Black and Low 1983; Healey 1991; King and Beamish 2000). In the Strait of Georgia, the main ctenophore genus utilized is *Pleurobrachia* (C. Cooper, 5953 Vermillion Place, Nanaimo,

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Table 1. Summary of experimental methods and results.

Age group	Sample size	FL (cm)	Prey	Prey wet mass (mg)	Feeding method	Digestion time	Results (mean ± 2 SE)
Age 0	5	10–12	*P. bachei*	144–360	Freely feeding	1 h	3.9 ± 3.2% remaining after 1 h
Age 0	10	10–12	Shrimp pieces	207–396	Freely feeding	1 and 5 h	87 ± 11% remaining after 1 h
Age 1	11	24–28	Shrimp pieces	254–399	Freely feeding	1 and 5 h	99 ± 2.8% remaining after 1 h
Age 0	19	12–14	*P. bachei*	144–274	Force-fed	5, 15, 35, and 60 min	6.9 ± 2.6% remaining after 1 h (see curve, Fig. 2)
Age 1	30	22–29	*P. bachei*	168–295	Force-fed	2, 10, 20, 35, 60, and 180 min	42 ± 8.0% remaining after 1 h (see curve, Fig. 2)
Age 1	10	—	*A. victoria* halves	500–3000	Placed in stomach fluid	Continual observation	Digestion within 2 min observed microscopically

Note: SE, standard error; FL, fork length.

BC V9V 1K2, personal communication). On the high seas, chum salmon stomachs often contain an unidentifiable amorphous mass of white to red jelly. However, in freshly caught fish, it may be possible to identify hydrozoa such as *Aglantha digitale* (O.F. Müller) or ctenophore such as *Beroe* sp. (Tsuruta 1963; Volkov et al. 1997).

Fish utilizing coelenterates typically have an enlarged digestive tract and pharyngeal or oesophageal modifications, presumably to prevent regurgitation (Purcell and Arai 2001). Chum salmon show such modifications. In chum salmon, the stomach is enlarged compared with other species of *Oncorhynchus*, occupying most of the coelomic cavity, and the walls are formed of a thick, soft tissue with low muscle tone (Welch 1997). The oesophagus is strongly muscular with a well-defined sphincter (Azuma 1992). Digestion and evacuation rates of chum salmon had previously been examined only for brine shrimp and moist pellets in the laboratory (Koshiishi 1980) or for mixed prey in the field (Azuma 1992, 1995; Hiramatsu et al. 1997). Digestion of other prey types by other *Oncorhynchus* species has been studied (e.g., of euphausiids by coho salmon (*Oncorhynchus kisutch*; Brodeur and Pearcy 1987) but not of any gelatinous prey.

As noted above, we know of no digestion data for any predator fish species feeding on any gelatinous prey taxon. The present laboratory study primarily investigated the digestion of the ctenophore *Pleurobrachia bachei* by age-0 and age-1 chum salmon, but we also examined the digestion of portions of the hydromedusa *Aequorea victoria*, a cnidarian, and shrimp (to provide a comparison with an arthropod, another prey group).

Material and methods

Age-0 *O. keta* were obtained at the Nitinat Fish Hatchery in June 2000. They were raised in a 5000-L aquaculture tank at the Pacific Biological Station on a diet of commercial pelleted food for Pacific salmon (EWOS Vector or EWOS Pacific). In experiments, they were used as age-0 fish (≥10-cm fork length (FL)) or retained in the tank overwinter and used as age-1 fish (≥22-cm FL) in 2001. Salmon were maintained in aquarium tanks at 13°C during acclimation and experiments. Fish were acclimated at least 3 days before feeding experiments and were starved for the last 2 days.

Pleurobrachia bachei and *A. victoria* were dipped from near-surface waters in Departure Bay (49°13′N, 123°57′W) or Ladysmith Harbour (48°59′N, 123°47′W), British Columbia, using 1-L glass containers attached to 2-m rods. They were maintained in 1-gallon glass jars on a diet of newly hatched *Artemia*, which was discontinued ≥24 h before they were used as prey. For experiments with freely feeding fish, the polar diameter (7–9 mm) of each *P. bachei* was measured before feeding, and the wet weight (144–360 mg) was calculated from a previously determined ordinary least squares relationship, $W = 1.005D^{2.553}$, estimated from a separate subsample of 23 animals. Shrimp (*Pandalus* sp.) used as prey were bought frozen. They were thawed and sections of the abdomen including cuticle were cut and weighed before feeding.

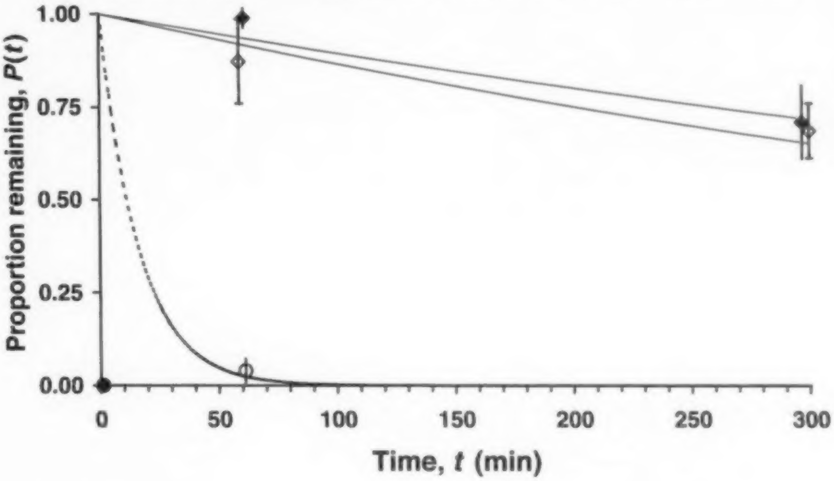
Two series of experiments were carried out (Table 1). In one series, freely feeding age-0 and age-1 fish were offered single premeasured *P. bachei* or preweighed shrimp pieces. The fish were individually monitored at 10-min intervals until feeding was observed, and the digestion period was calculated starting from the middle of the observation interval. In the second series, age-0 and age-1 fish were force-fed reweighed *P. bachei* or portions (usually a hemispherical half animal) of the hydromedusa *A. victoria*.

In force-feeding experiments, the chum were removed from the water and preweighed prey were placed in the mouth and then gently pushed down into the stomach using a glass rod. Greater resistance was present in age-1 than in age-0 fish, presumably because of greater development of the oesophageal sphincter. Nevertheless, in preliminary trials, no splitting of the external surface of whole ctenophores was evident during this procedure provided that a wide rod was used.

After feeding and a digestion period, the fish were sacrificed and the stomach was removed. The contents were placed in a preweighed petri dish and weighed to the nearest 0.1 mg. The proportion of prey weight remaining was calculated and plotted against time. The instantaneous rate of digestion was calculated by log-transforming the proportion of prey remaining (P) at time (t) and then fitting a linear regression to the transformed data with intercept fixed at 1. The slope of this relationship (r) defines the exponential rate of decay in an initial mass of food with time, $P(t) = P(0)e^{-rt}$.

To compare the rates of digestion of a different gelatinous organism, portions of the hydromedusa *A. victoria* were also force-fed to age-1 chum. In these experiments, substantial water was lost from the gastrovascular system during preparative cutting of the medusa, with further loss during force-feeding, making it impossible to obtain quantitative data on actual digestion. Therefore, to examine this further,

Fig. 1. Digestion of *Pleurobrachia bachei* and pieces of shrimp (*Pandalus* sp.) by freely feeding *Oncorhynchus keta*; proportion of mass remaining 1 and 5 h after feeding: ◇, shrimp in age-0 *O. keta* ($n = 10$); ◆, shrimp in age-1 *O. keta* ($n = 10$); ○, *P. bachei* in age-0 *O. keta* ($n = 5$). Digestion curves are calculated as reported in the text; observed values are shown ±2 SE.



we placed portions of medusa in freshly dissected age-1 chum stomachs and followed the progress of digestion microscopically.

Results

In freely feeding experiments, live *P. bachei* were presented to age-0 chum salmon in 2000 (see Table 1 for data summary). These fish were only approaching the 13-cm FL at which chum in the field have been reported to switch to predation on larger prey items. Nevertheless, when several fish were individually monitored at 10-min intervals after the ctenophores were offered, five fish did feed and were sacrificed after 1 h (Fig. 1). Chum from the same group of fish did not voluntarily feed on *P. bachei* in 2001 after being held over winter and fed on pellets.

Preweighed pieces of shrimp abdomen with cuticle attached were also offered to two groups of age-0 fish, which were sacrificed 1 or 5 h after feeding ($n = 5$ per group). A marked difference from the ctenophores was evident in the rate of digestion (Fig. 1; Table 1) with 3.9% of the ctenophore remaining at 1 h, but 87% of the shrimp remaining after 1 h and 69% remaining after 5 h. These values correspond to instantaneous rates of digestion of ctenophores of $r = -0.061\ \mathrm{h}^{-1}$ and of shrimp $r = -0.0013\ \mathrm{h}^{-1}$. Thus over the 1-h period approximately 22 times more shrimp weight than ctenophore weight remained in the stomach. Similar experiments feeding shrimp pieces to age-1 fish ($N = 11$ per group) showed very similar rates of digestion to age-0 fish ($r = -0.0011\ \mathrm{h}^{-1}$; Fig. 1).

To examine the progress of digestion more exactly, we also force-fed preweighed *P. bachei* to age-0 chum and sacrificed them at shorter intervals (Fig. 2). Each point is based on five fish except at 35 min (four fish). The results at 1 h were consistent with the first experiment, although early digestion was most rapid ($r = -0.1096\ \mathrm{h}^{-1}$); more than half of the mass of the ctenophore was lost within 5 min.

The experiments force-feeding *P. bachei* were repeated using age-1 chum salmon in 2001 (Fig. 2). The digestion rate was slower than that of the age-0 ($r = -0.0101\ \mathrm{h}^{-1}$), although still faster than digestion following voluntarily feeding on shrimp. The digestion of the hydromedusa *A. victoria* was also very rapid. As noted in the Material and methods, it was not possible to obtain quantitative data on the rate of digestion because of substantial water loss when *A. victoria* was cut into pieces small enough to be ingested, but partial digestion of the tentacles on the bell rim could be seen microscopically after only 2 min.

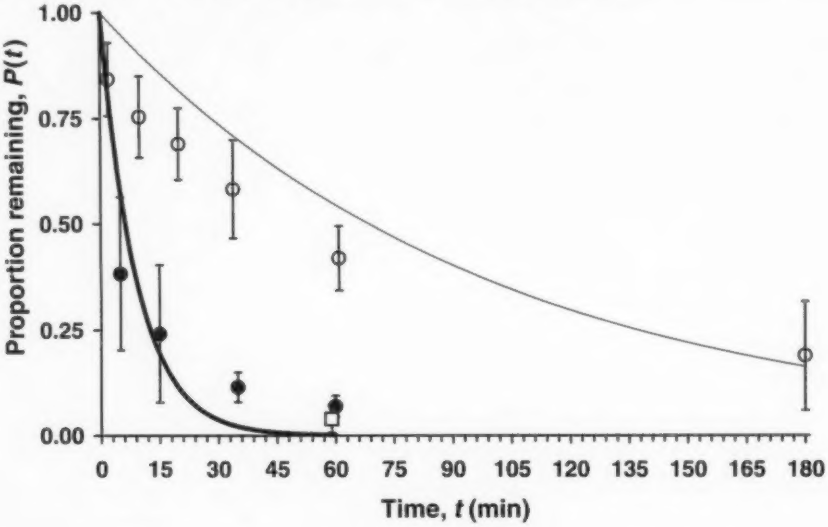
Discussion

The gastric evacuation rate of salmonids, as with other fish, is affected by various factors such as water temperature, food size and type, and fish size (Suzuki 1993). The methods used in previous studies of chum salmon digestion mentioned in the Introduction differ from those used in the present study, so direct comparison is not possible. Nevertheless, in those studies, reported digestion times for either pelleted food or mixed diets were measured in hours, as we observed for shrimp, rather than minutes, as found with the coelenterate diets.

In both age classes, we observed that the simple exponential regression underestimated the initial rate of digestion of *P. bachei* in the chum salmon stomach, suggesting that the prey weight loss may occur in several stages rather than in a simple exponential decay process. This could be due to rates of digestion being different for ctenophore tissues of varying composition, to the multiple enzyme systems of the chum salmon operating at different rates or stages of digestion, or possibly also to early expression of water from the gastrovascular cavity of *P. bachei*.

It is not known why the digestion of *P. bachei* was slower in the age-1 than in the age-0 chum salmon, although digestion of shrimp did not differ significantly between the two ages. One possibility is that there was a difference in pro-

Fig. 2. Digestion of *Pleurobrachia bachei* by force-fed *Oncorhynchus keta*; proportion of mass remaining examined at shorter time intervals than in the freely feeding experiments: ●, the results for 19 age-0 fish force-fed in 2000; ○, the results for 30 of the same group force-fed at age-1 in 2001. For comparison, the square (□) indicates the digestion rate in a freely feeding trial conducted in 2000. Digestion curves are calculated as reported in the text; observed values are shown ±2 SE.



duction of some digestive enzyme of more importance to coelenterate digestion. This might occur either as a result of developmental changes with age or as a result of the use of a standard maintenance diet of commercial fish pellets over the winter.

Two types of the proteolytic enzyme pepsin have been identified in chum stomachs (Sanchez-Chiang et al. 1987). One of these is produced by age-0 fish in estuaries and is continued into the adult stage in salt water, and a second, which is activated by sodium chloride, is also present in the older fish. The exact timing of changes in enzyme production is unknown. The composition of ctenophores and hydromedusae, as well as crustacea, is proportionally high in protein compared with lipid or carbohydrate (see, for example, a summary of various species in Bailey et al. (1995)). Age-related production of other digestive enzymes might therefore be of more importance in allowing changes in digestion of coelenterates without changes in digestion of arthropods. A possibility might be hyaluronidase, a mucopolysaccharidase that is present in the stomachs of some other fish including the mackerel *Scomber japonicus*, which also eats gelatinous prey (Kitamikado and Yamamoto 1972). Unfortunately, these enzymes have not yet been investigated in chum salmon.

The fast digestion rates demonstrated in this study emphasize the need to immediately examine the stomach contents of fish caught in the field in order to document feeding on coelenterates. Given the high rate of digestion observed, fish that are frozen and thawed, or for which whole stomachs are placed in preservative, will already have lost much of their coelenterate content when examined. With mixed diets, this necessity for rapid inspection is increased by the difficulty of recognizing partially digested gelatinous material among other prey. An alternative compromise to immediate observation may be to inject fixative directly into the stomach as soon as the fish are brought on board. However, many ctenophores and hydromedusae disintegrate in fixative and even comparatively robust species may shrink. For example, *Pleurobrachia pileus* placed in 4% formaldehyde–seawater solution shrink 8–13% almost immediately and continue to shrink over the next year (Yip 1982). Similar shrinkage occurs even in borax-buffered formaldehyde (Mutlu 1996).

Biologists studying the food habits of fish have tended to assume that gelatinous organisms, with their high water and salt content relative to organic content, are poor food. The energy contents of coelenterates have been difficult to measure, especially in species with proportionately large amounts of mesoglea as a result of the high amount of salt and hence of bound water (Arai 1997). Reported calorimetric values for energy contents of hydromedusae and ctenophores typically range from 90 to 200 cal·g^{-1} wet weight (1 cal = 4.1868 J) or less than 20% of the caloric value of arthropods (Arai 1988; Davis et al. 1998).

We have measured rates of ctenophore digestion over 20 times the rate of digestion of shrimp by the same fish species. Although only qualitative observations were made, it is apparent that the digestion of hydromedusae is also very rapid. These results suggest that the measured mass of different organisms in the stomachs of predators should be scaled by their relative rates of digestion. On this basis, given the very high rate of digestion (and presumably assimilation) observed for ctenophores, coelenterates may equal or even exceed arthropods in relative importance as an energy source. The use of unscaled prey weights in predator stomachs to infer the importance of different components of the food web may significantly underestimate the importance of gelatinous zooplankton in marine food chains. In the last 15 years, coelenterates have been recognized in the diets of increased numbers of common fish species (Ates 1988; Arai 1988; Brodeur and Pearcy 1992). As discussed by Mianzan et al. (1996) and Purcell and Arai (2001), the challenge now is to investigate their quantitative importance.

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Recruitment dynamics of walleyes (*Stizostedion vitreum*) in Kansas reservoirs: generalities with natural systems and effects of a centrarchid predator

Michael C. Quist, Christopher S. Guy, and James L. Stephen

Abstract: Knowledge of factors influencing recruitment dynamics of walleyes (*Stizostedion vitreum*) in different systems and regions is important for developing a better understanding of walleye ecology. Therefore, we investigated associations among walleye recruitment and climatic, water-level, and biotic characteristics in four Kansas reservoirs during 1985–1999. Walleye recruitment was positively related to spring storage ratios and temperatures and negatively associated with spring water levels and abundance of 130- to 199-mm white crappies (*Pomoxis annularis*). The influence of juvenile white crappie predation on larval walleyes was examined by conducting a manipulative experiment. Regardless of zooplankton density or water clarity, mortality of larval walleyes resulting from white crappie predation was over 90%. Based on our empirical and experimental results, we propose a biotic–abiotic confining hypothesis (BACH) to explain abiotic and biotic effects on walleye recruitment dynamics. Specifically, high variability in walleye recruitment was observed during years with low densities of 130- to 199-mm white crappies and likely resulted from the effects of abiotic factors. When white crappie abundance was high, walleye recruitment was low and exhibited little variability, suggesting that white crappies can have an overriding influence on walleye recruitment regardless of abiotic conditions.

Résumé : Une connaissance des facteurs qui influencent la dynamique du recrutement des dorés jaunes (*Stizostedion vitreum*) dans divers systèmes et régions est nécessaire pour mieux comprendre l'écologie de ce poisson. Nous avons donc étudié les associations entre le recrutement du doré et les caractéristiques du climat et du niveau de l'eau, ainsi que les caractéristiques biotiques, dans quatre réservoirs du Kansas de 1985 à 1999. Le recrutement du doré est en relation positive avec les coefficients de stockage au printemps et les températures et en relation négative avec les niveaux d'eau au printemps et l'abondance des mariganes blanches (*Pomoxis annularis*) de 130–199 mm. Une expérience de manipulation a permis de déterminer l'influence de la prédation des jeunes mariganes sur les larves de dorés. Quelle que soit la densité du zooplancton ou la clarté de l'eau, la mortalité des larves de dorés due aux mariganes est supérieure à 90 %. D'après nos résultats empiriques et expérimentaux, nous proposons une hypothèse BACH (hypothèse contraignante biotique–abiotique) pour expliquer les effets abiotiques et biotiques sur la dynamique de recrutement des dorés. Plus spécifiquement, il y a une forte variabilité dans le recrutement des dorés durant les années de faible abondance de mariganes de 130–199 mm qui résulte sans doute des effets des facteurs abiotiques. Lorsque l'abondance des mariganes est élevée, le recrutement des dorés est faible et peu variable, ce qui fait croire que les mariganes ont une influence prépondérante sur le recrutement des dorés, quelles que soient les conditions abiotiques.

[Traduit par la Rédaction]

Introduction

The mechanisms whereby similar species coexist remain under debate (Huisman and Weissing 2000). Many researchers suggest that if species are too similar in resource use, they cannot coexist indefinitely and species that do coexist in nature do so by partitioning resources (Vermeij 1994). One of the important theories regarding the coexistence of species is

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that enemy-related (i.e., competitors and predators) adaptations have brought about long-term evolutionary trends in organisms such that competition and predation are reduced (Vermeij 1994; Huisman and Weissing 2000). These adaptations may include differing morphologies and habitat use or changes in the timing of major life history events (e.g., spawning, diet shifts) that allow for resource partitioning (Werner and Gilliam 1984). If species are able to coexist because of their long evolutionary histories, then an obvious question arises in systems where species have been introduced into unique habitats and communities — how do competitors and predators interact when they have little or no history of co-occurrence?

In natural lake and river ecosystems, a dynamic equilibrium has developed over thousands of years among the physical, chemical, and biological characteristics of the system (Noble 1986). Consequently, fish communities are well structured in natural systems provided that there has been a long evolutionary history of predator and prey assemblages (MacLean and Magnuson 1977). Conversely, reservoirs are typically less than 70 years old (Thornton et al. 1990) and represent novel habitats for fishes. Most reservoirs in the U.S. are concentrated in southern latitudes, whereas most natural lakes are located in the northern glaciated regions; therefore, reservoirs tend to be warmer and shallower than natural lakes and have longer growing seasons (Thornton et al. 1990). Reservoirs also tend to display high nutrient and sediment inputs and experience frequent water-level fluctuations. In addition to unique abiotic conditions, reservoir fish communities usually consist of species with little or no evolutionary history of cooccurrence.

Walleyes (*Stizostedion vitreum*), white crappies (*Pomoxis annularis*), white bass (*Morone chrysops*), and gizzard shad (*Dorosoma cepedianum*) are important consumers in aquatic systems throughout much of North America. The native distribution of walleyes is generally limited to the natural lakes and rivers of Canada and the northern U.S. (Colby et al. 1979; Carlander 1997), whereas that of white crappies, white bass, and gizzard shad encompasses the midwestern and southern U.S. (Lee et al. 1980). After the completion of large-scale reservoir construction during the 1940s to 1970s, introductions expanded the distribution of walleyes to include most of North America (Carlander 1997). Because the ontogeny of walleyes has been shaped by their long evolutionary history with the chemical, physical, and biological characteristics of natural lakes and rivers (MacLean and Magnuson 1977), understanding how walleye populations respond to the unique abiotic conditions and biotic interactions in reservoirs is important for predicting population and community dynamics.

Recruitment is often cited as the governing and most variable component of fish population dynamics (Gulland 1982). Thus, understanding mechanisms responsible for variations in recruitment of walleyes has been the focus of many applied and basic ecological studies (Colby et al. 1979; Carlander 1997; Hansen et al. 1998). Although previous studies have been conducted in a variety of ecosystems (e.g., natural lakes, rivers, reservoirs), several generalizations have emerged regarding the factors affecting walleye recruitment dynamics. The most common factors associated with walleye recruitment variability are water temperature, wind, and water-level characteristics (Colby et al. 1979; Carlander 1997). For example, spring temperatures may influence walleye recruitment dynamics by altering the time of spawning, duration of egg incubation, or the growth of larvae (Busch et al. 1975; Colby et al. 1979). Prolonged incubation periods may expose eggs to high winds, causing dislodgement or stranding of eggs (Busch et al. 1975). Wind-generated water currents may also concentrate larvae in habitats that are unsuitable for growth and survival (Noble 1972). In addition to abiotic constraints, biotic interactions, such as competition, cannibalism (Forney 1980), and interspecific predation (Schiavone 1985), may have a negative effect on walleye recruitment.

Although recruitment dynamics of walleyes have been extensively studied, most of our knowledge has emerged from research on native populations in natural systems (Colby et al. 1979; Carlander 1997). Comparatively few studies on walleye recruitment have been conducted in systems outside their native distribution, despite the importance of understanding how introduced walleye populations respond to abiotic conditions and biotic interactions characteristic of reservoirs. Therefore, the objectives of this study were to examine the importance of abiotic factors and biotic interactions on walleye recruitment in several southern Great Plains reservoirs. Specifically, we investigated the influence of climatic factors and water-level characteristics on walleye recruitment dynamics to determine if the same factors (e.g., thermal and water-level characteristics) that are important for walleye recruitment in native populations can be generalized to Kansas reservoirs. Intraspecific and interspecific interactions (i.e., white crappie, white bass, gizzard shad) were examined to determine the role of biotic factors on walleye recruitment dynamics. In addition, a manipulative experiment was conducted to identify mechanisms that influence larval walleye survival in the presence of white crappies.

Materials and methods

Study area

We selected four Kansas reservoirs (Table 1) as our study system based on their similarity to reservoirs throughout Kansas and availability of long-term information. Walleyes were introduced to Kansas reservoirs in the 1940s and are currently one of the most popular sport fish in Kansas. Kansas reservoirs are unique systems with respect to the ecology of walleyes, not only because they are artificial, but also because the highly variable climate of the southern Great Plains results in frequent water-level fluctuations and high summer water temperatures (i.e., >30°C; Quist et al. 2002). Nearly all of the reservoirs are U.S. Bureau of Reclamation projects and are used for flood control and irrigation. Similar to other Great Plains reservoirs (Thornton et al. 1990), the study reservoirs are shallow and turbid and rarely thermally stratify because of persistent, high winds. Sport fish populations are dominated by white bass, walleyes, white crappies, and channel catfish (*Ictalurus punctatus*). Gizzard shad are the primary prey species in all reservoirs (Quist et al. 2002).

Biotic interactions and abiotic conditions

Fish populations were sampled yearly in each reservoir from 1985 to 1999 using standardized fall (i.e., October and November) samples. Catch rates of walleyes (age 0, <300 mm; age 1 and older, >300 mm; Quist et al. 2003),

Table 1. Surface area (SA; ha), mean depth (m), watershed area (WA; km^2), and shoreline development index (SDI) for Kansas reservoirs used in analysis of walleye recruitment variation during 1985–1999.

Reservoir	SA	Depth	WA	SDI
Glen Elder	5093	5.8	17 702	3.9
Kirwin	2055	5.9	3 540	3.7
Webster	1513	6.6	2 978	5.8
Wilson	3642	8.8	4 965	7.5

Note: SDI = shoreline length/(2(SA × π)^{½}.

white bass (age 0, <250 mm; age 1 and older, >250 mm; Guy et al. 2002), and adult gizzard shad (age 1 and older, >125 mm; Quist et al. 2001) were calculated from gill net complements (catch-per-unit-effort (CPUE) = number per gill net complement night (NCN); Table 2). One gill net complement consisted of four separate gill nets (30.5 m long × 2.4 m deep sinking gill nets), each with a different mesh size (2.5-, 3.8-, 6.4-, and 10.2-cm bar-measure mesh). All gill net complements were set during the evening and allowed to fish until the following morning. Recruitment of walleyes was assessed using CPUE of age-0 walleyes. Preliminary analysis determined that CPUE of age-0 walleyes provides an excellent index for recruitment to later ages (CPUE of age-1 walleyes in year $t + 1 = \beta_0 + \beta_1 \times$ CPUE age-0 walleyes in year t; $r^2 = 0.74$ to 0.96, $P = 0.05$ to 0.007 by reservoir). Similar results were reported by Willis and Stephen (1987) for Kansas reservoirs.

Abundance of white crappies and juvenile gizzard shad (age 0, <125 mm; Quist et al. 2001) was assessed using data from fall trap net samples (CPUE = number per trap net night (TNN); Table 2). Trap nets (1.2 m × 1.5 m frame; 15.2 m long × 1.8 m deep lead) were fished overnight during October and November. Trap nets with 2.5-cm mesh were the standard gear for sampling white crappies in all reservoirs until 1985 and are currently used intermittently in a few reservoirs; however, we limited our analysis to white crappies sampled in trap nets with 1.3-cm mesh (i.e., 1985–1999). CPUE of white crappies was refined by calculating CPUE by length category (Table 2). These length categories correspond to age-0 (<130 mm), age-1 (130–199 mm), and age-2 and older (>200 mm) white crappies (M.C. Quist, unpublished data).

Precipitation (mm·day^{-1}), air temperature (°C), and wind speed (m·s^{-1}) data were obtained from National Oceanic and Atmospheric Administration weather stations in Russell, Kansas. Distance from the study reservoirs to the weather station varied from 40 to 140 km (mean ± standard error (SE); 90.1 ± 21.4 km). Climatic data were summarized by time period: month, season (winter = December through February, spring = March through May, summer = June through August, fall = September through November), and year (Table 2). Reservoir elevation (metres above mean sea level (m msl)) and outflow (m^3·s^{-1}) data were obtained from the U.S. Army Corps of Engineers and U.S. Bureau of Reclamation. Reservoir elevations and storage ratios (SR = volume at conservation pool/reservoir discharge volume) were also summarized by month, season, and year.

Multiple regression analysis was used to explore factors related to walleye recruitment dynamics. CPUE of age-0 walleyes (i.e., $\log_{10}$(CPUE +1)) was plotted against abiotic and biotic (i.e., $\log_{10}$(CPUE +1)) data to determine which variables exhibited trends with walleye recruitment in each reservoir. After potentially important variables were identified, stepwise multiple-regression analysis was conducted for each reservoir using a backward selection procedure (Ott 1993). Although the selection procedure was used to identify the best model for each reservoir (i.e., highest R^2), other variables not included in the selection procedure were iteratively added to each model to examine their contribution. The contribution of individual variables was then tested using F tests, and regression equations were limited to variables that contributed significantly ($P < 0.05$) to the model. Each model was also compared with a reduced model (e.g., four-variable model versus three-variable model) using an F test based on reductions in the residual sums of squares (Milliken and Johnson 1992):

$$F = [(\mathrm{RSS_{red}} - \mathrm{RSS_{full}})/(\mathrm{df_{red}} - \mathrm{df_{full}})](\mathrm{RSS_{full}}/\mathrm{df_{full}})^{-1}$$

where RSS represents residual sums of squares for the reduced ($\mathrm{RSS_{red}}$) and full ($\mathrm{RSS_{full}}$) models and df is degrees of freedom (df = sample size – number of parameters – 1) of the reduced ($\mathrm{df_{red}}$) and full ($\mathrm{df_{full}}$) models. The F value is compared with $F_{[0.05,1,\mathrm{df_{full}}]}$ to test the null hypothesis that the reduced model is significantly better than the full model. Multicollinearity was assessed by examining tolerance values and variance inflation factors as recommended by Sokal and Rohlf (1995). Multicollinearity was not observed among variables in any of the final models. In addition to developing regression models separately for each reservoir, an overall model using data from all reservoirs was developed using standardized values (i.e., z scores) of each variable (Ott 1993). In the final regression models, squared partial correlation coefficients (r^2_{partial}) were estimated as sums of squares for the variable (SS) divided by the error sums of squares (SSE) plus the sums of squares for the variable (i.e., $r^2_{\mathrm{partial}} = \mathrm{SS}(\mathrm{SSE} + \mathrm{SS})^{-1}$; Freund and Littell 1991).

Mesocosm experiment

The influence of juvenile white crappie predation on walleye survival was examined by conducting a manipulative experiment. Experiments were conducted at Milford Fish Hatchery (MFH; Junction City, Kansas) in cylindrical, polyethylene mesocosms (2.2 m diameter × 1.1 m deep; 4190-L capacity). Although the primary purpose of the experiment was to determine if juvenile white crappie consume larval walleyes, we were secondarily interested in the effect of reduced water clarity and alternative prey (i.e., zooplankton) densities as a buffer against predation. Larval walleyes were obtained directly from MFH, whereas water, zooplankton, and white crappies were obtained from the MFH supply lake. The MFH supply lake is a 41-ha reservoir used primarily as a water source for fish hatchery operations, but it also provides a recreational fishery because of abundant white crappie, channel catfish, and white bass populations.

Three zooplankton treatments (low, intermediate, and high) were examined. The low zooplankton density treatment reflected ambient zooplankton densities of the MFH supply

Table 2. Abiotic and biotic variables used to examine relationships in walleye recruitment in four Kansas reservoirs during 1985–1999.

Variable	Temporal scale	Statistics
Abiotic		
Temperature	Month, season, year	Mean, CV, warming rate
Reservoir elevation	Month, season, year	Mean, CV
Precipitation	Month, season, year	Mean, CV
Wind speed	Month, season	Mean, CV
Biotic		
Walleye ≥300 mm	Fall sampling	Gill net CPUE
White crappie <130 mm	Fall sampling	Trap net CPUE
White crappie 130–199 mm	Fall sampling	Trap net CPUE
White crappie ≥200 mm	Fall sampling	Trap net CPUE
White bass <250 mm	Fall sampling	Gill net CPUE
White bass >250 mm	Fall sampling	Gill net CPUE
Gizzard shad <125 mm	Fall sampling	Trap net CPUE
Gizzard shad >125 mm	Fall sampling	Gill net CPUE

Note: Abiotic variables were summarized by estimating the mean and coefficient of variation (CV = $100 \cdot \text{std.dev.} \cdot \text{mean}^{-1}$) by month, season (winter = December through February, spring = March through May, summer = June through August, and fall = September through November), and year. Abiotic variables included air temperature (°C), reservoir elevation (metres above mean sea level), precipitation (mm), and wind speed ($\text{m} \cdot \text{s}^{-1}$). Warming rate was estimated as the temperature change per day ($^\circ\text{C} \cdot \text{day}^{-1}$) between 1 April and 15 May. Biotic data represent catch-per-unit-effort in gill nets (CPUE = fish per gill net complement night) or trap nets (CPUE = fish per trap net night).

lake, whereas elevated densities (i.e., intermediate and high treatments) were obtained by adding zooplankton collected with a conical net (0.5 m diameter × 1.5 m long, 500-μm mesh) towed for either 5 min (intermediate treatment) or 10 min (high treatment). Zooplankton treatments were randomly assigned to each of the mesocosms, and two juvenile white crappies (157.9 ± 5.4 mm) were stocked into each mesocosm. White crappies were allowed to acclimate for at least 24 h before the addition of larval walleyes. After 24 h, 10 larval walleyes (7.1 ± 0.6 mm) were added to each mesocosm. The experiment ran for 8 h and then white crappies were removed and euthanatized. The stomach from each white crappie was removed and preserved in 10% formalin to confirm predation on larval walleyes. Mesocosms were drained through 500-μm mesh to retrieve remaining walleyes. Zooplankton samples were collected before stocking walleyes using a conical plankton net (0.1 m diameter × 0.3 m long, 80-μm mesh) and preserved in 70% ethanol. Zooplankton were enumerated by counting all organisms in a 5-mL subsample. Water temperature (°C) and dissolved oxygen ($\text{mg} \cdot \text{L}^{-1}$) were measured twice during the experiment using a multiprobe (model 85; Yellow Springs, Inc., Yellow Springs, Ohio) and turbidity (nephelometric turbidity units (NTU)) was measured before stocking walleyes in each mesocosm using a turbidimeter (model 2100P; Hach Company, Loveland, Colo.). Control experiments were conducted using the same methods except that white crappies were not added to mesocosms. Each treatment was replicated seven times.

Multivariate analysis of variance (MANOVA; Johnson 1998) was first used to determine if the dependent variables (mean zooplankton densities (number per litre of total zooplankton and *Daphnia* spp.), turbidity) differed among treatments (i.e., low, intermediate, and high zooplankton density). One-way analysis of variance (ANOVA) was performed on each variable because the MANOVA indicated that treatments were different for one or more of the variables (Wilks' $\lambda = 0.01$, $F_{[8,30]} = 30.4$, $P = 0.0001$; Milliken and Johnson 1992; Johnson 1998). When one-way ANOVA models were significant, multiple comparisons were conducted using least-squares means. Differences in mean walleye mortality, expressed as a proportion (%), were assessed using a Kruskal–Wallis test.

Results

Empirical associations

Walleye recruitment was related to a variety of abiotic and biotic variables among reservoirs (Table 3). A significant four-variable model was developed for all reservoirs except Wilson Reservoir; however, the four-variable model did not provide a significantly better fit than the three-variable model for each reservoir ($F_{[1,7 \text{ to } 9]} = 0.99\text{–}4.40$, $P < 0.05$). Similarly, three-variable models provided a significantly better fit than two-variable models in each reservoir ($F_{[1,8 \text{ to } 10]} = 4.33\text{–}11.08$, $P < 0.05$). In Glen Elder and Webster reservoirs, walleye recruitment was positively associated with spring storage ratio and negatively related to spring elevation and catch rates of 130- to 199-mm white crappies (Table 3). Based on the squared partial correlation coefficients, spring storage ratio appeared to have the largest influence on the model for Glen Elder, followed by spring elevation and juvenile white crappie abundance. In Kirwin and Wilson reservoirs, high catch rates of age-0 walleyes occurred during years with warm spring temperatures, high storage ratio, and low catch rates of 130- to 199-mm white crappies (Table 3). White crappie abundance and spring storage ratios had the highest squared partial correlation values, followed by mean spring temperatures in both reservoirs. When data from all reservoirs were combined, high walleye recruitment was related to high spring storage ratios and low abundance of

Table 3. Multiple regression models developed to assess factors influencing catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes ($\mathrm{WAE} = \log_{10}(\mathrm{CPUE} + 1)$) in four Kansas reservoirs during 1985–1999.

	r^2_{partial}					Model statistics		
Model	Temp.	Wind	WHC	SR	Elev.	RSS	R^2	P
Glen Elder Reservoir ($N = 12$)								
$\mathrm{WAE} = -118.378 + 0.047(\mathrm{Temp.}) - 0.216(\mathrm{WHC}) + 1.338\ (\mathrm{SR}) - 0.260(\mathrm{Elev.})$	0.15		0.22	0.55	0.43	0.121	0.68	0.045
$\mathrm{WAE} = -101.459 - 0.211(\mathrm{WHC}) + 1.228(\mathrm{SR}) - 0.221(\mathrm{Elev.})$[a]			0.32	0.56	0.42	0.191	0.66	0.026
$\mathrm{WAE} = -56.8761 + 0.611(\mathrm{SR}) - 0.129(\mathrm{Elev.})$				0.15	0.06	0.370	0.15	0.27
$\mathrm{WAE} = 0.714 + 0.387(\mathrm{SR})$						0.489	0.10	0.20
Kirwin Reservoir ($N = 13$)								
$\mathrm{WAE} = 8.132 + 0.115(\mathrm{Temp.}) - 0.289(\mathrm{Wind}) - 0.378(\mathrm{WHC}) + 0.003(\mathrm{SR})$	0.29	0.21	0.72	0.42		0.675	0.74	0.007
$\mathrm{WAE} = 9.926 + 0.148(\mathrm{Temp.}) - 0.477(\mathrm{WHC}) + 0.004(\mathrm{SR})$[a]	0.27		0.65	0.48		0.759	0.71	0.008
$\mathrm{WAE} = 8.211 - 0.467(\mathrm{WHC}) + 0.003(\mathrm{SR})$			0.32	0.47		1.297	0.52	0.01
$\mathrm{WAE} = 7.049 - 0.346(\mathrm{WHC})$						2.680	0.15	0.19
Webster Reservoir ($N = 14$)								
$\mathrm{WAE} = -118.138 + 0.274(\mathrm{Temp.}) - 1.221(\mathrm{WHC}) + 0.007(\mathrm{SR}) - 0.203(\mathrm{Elev.})$	0.48		0.67	0.72	0.54	0.830	0.70	0.01
$\mathrm{WAE} = -87.340 - 0.835(\mathrm{WHC}) + 0.008(\mathrm{SR}) - 0.154(\mathrm{Elev.})$[a]			0.48	0.48	0.27	1.061	0.65	0.01
$\mathrm{WAE} = 1.163 - 0.744(\mathrm{WHC}) + 0.003(\mathrm{SR})$			0.36	0.45		2.237	0.44	0.02
$\mathrm{WAE} = 0.706 + 0.002(\mathrm{SR})$						3.196	0.21	0.02
Wilson Reservoir ($N = 14$)								
$\mathrm{WAE} = -0.593 + 0.116(\mathrm{Temp.}) - 0.693(\mathrm{WHC}) + 0.649(\mathrm{SR})$	0.27		0.53	0.55		0.450	0.66	0.038
$\mathrm{WAE} = 0.515 - 0.434(\mathrm{WHC}) + 0.731(\mathrm{SR})$[a]			0.37	0.60		0.645	0.59	0.007
$\mathrm{WAE} = 0.582 + 0.419(\mathrm{SR})$						1.080	0.16	0.053
All reservoirs								
$\mathrm{WAE} = 10.220 + 1.884(\mathrm{Temp.}) - 0.135(\mathrm{WHC}) + 0.134(\mathrm{SR})$	0.04		0.10	0.22		12.541	0.31	0.003
$\mathrm{WAE} = 18.799 - 0.154(\mathrm{WHC}) + 0.082(\mathrm{SR})$[a]			0.09	0.23		12.616	0.29	0.002
$\mathrm{WAE} = 13.873 + 0.125(\mathrm{SR})$						15.431	0.13	0.004

Note: Independent variables include mean spring (March through May) temperature (Temp., °C), mean spring wind speed (Wind, $\mathrm{m \cdot s^{-1}}$), catch-per-unit-effort (CPUE = fish per trap net night) of 130- to 199-mm white crappies ($\mathrm{WHC} = \log_{10}(\mathrm{CPUE} + 1)$), spring storage ratio (SR = volume at conservation pool/reservoir discharge volume), and mean spring elevation (Elev., m). The best four-, three-, two-, and one-variable models (i.e., lowest residual sums of squares and highest R^2) are provided for each reservoir. Squared partial correlation coefficients (r^2_{partial}) and model statistics (RSS = residual sums of squares, R^2 = adjusted coefficient of determination) are provided for each model.

[a] The best model based on comparisons of residual sums of squares.

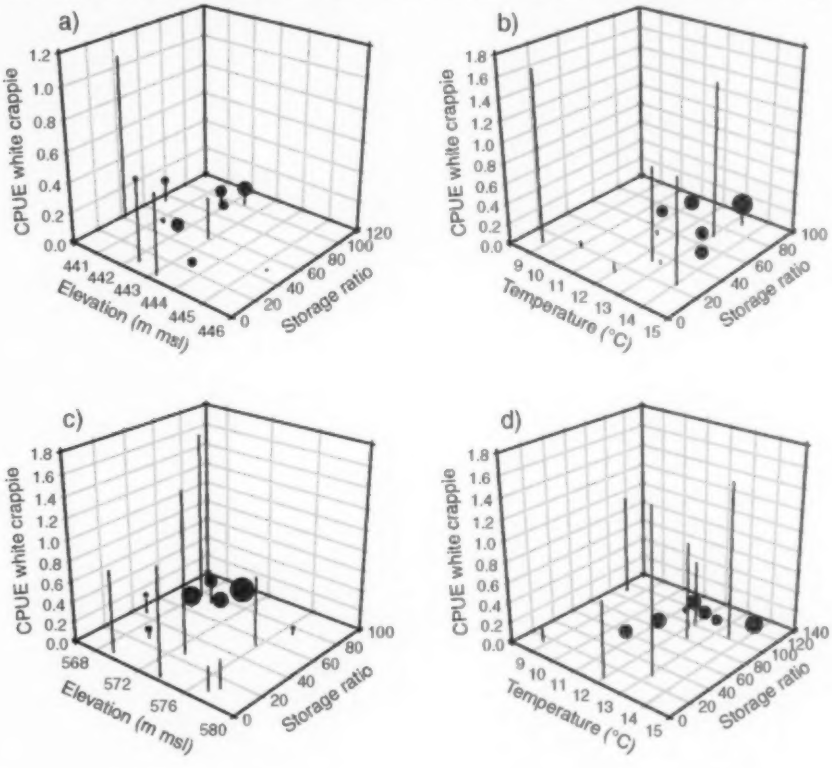
130- to 199-mm white crappies (Table 3). Regardless of abiotic conditions, walleye recruitment was low when juvenile white crappies were abundant (Fig. 1). For example, in Kirwin and Wilson reservoirs, years with high spring storage ratios and warm spring temperatures should have produced high catch rates of age-0 walleyes, but this was not observed when juvenile white crappie densities were high (Fig. 1). A similar relationship was observed using information from all reservoirs (Fig. 2). Therefore, white crappies appeared to have an overriding influence on walleye recruitment when juvenile white crappie densities were high.

Mesocosm experiment

Results from the mesocosm experiment corroborated the empirical observations. Water temperatures in the mesocosms averaged 15.5°C (SE = 0.1°C) and dissolved oxygen was above 8 $\mathrm{mg \cdot L^{-1}}$ (9.6 ± 0.1 $\mathrm{mg \cdot L^{-1}}$) during the experiment. Zooplankton communities in the low zooplankton treatment were dominated by copepod nauplii (mean frequency by number ± SE; 64.8 ± 0.5%), whereas *Daphnia* spp. (primarily *D. pulicaria* and *D. galeata*) dominated communities in the intermediate (53.0 ± 3.6%) and high (80.5 ± 0.9%) treatments. *Bosmina* spp. were common in all treatments and averaged 8.6% by number (SE = 2.4). Total zooplankton ($F_{[2,18]} = 36.5$, $P = 0.001$; low = 43.4 ± 3.6 $\mathrm{zooplankton \cdot L^{-1}}$, intermediate = 91.9 ± 6.2 $\mathrm{zooplankton \cdot L^{-1}}$, high = 187.5 ± 19.7 $\mathrm{zooplankton \cdot L^{-1}}$) and *Daphnia* spp. densities ($F_{[2,18]} = 60.5$, $P = 0.0001$; low = 3.4 ± 0.9 *Daphnia*$\cdot \mathrm{L^{-1}}$, intermediate = 53.2 ± 4.0 *Daphnia*$\cdot \mathrm{L^{-1}}$, high = 148.2 ± 15.8 *Daphnia*$\cdot \mathrm{L^{-1}}$) were significantly different among treatments and were almost 50 times higher in the high zooplankton treatment than in the low zooplankton treatment. Similar to zooplankton densities, turbidity differed among treatments ($F_{[2,18]} = 603.8$, $P = 0.0001$; low = 20.1 ± 1.8 NTU, intermediate = 36.0 ± 0.5 NTU, high = 60.4 ± 1.2 NTU), indicating that our method of supplementing zooplankton not only elevated zooplankton densities, but also significantly reduced water clarity.

Control experiments without white crappies indicated that retrieval of larval walleyes averaged 90% (SE = 5.8%; Fig. 3). Therefore, missing walleyes were assumed to have been consumed by white crappies. Walleye mortality averaged 93.6% (SE = 0.9) and did not differ among treatments (Kruskal–Wallis statistic, $H = 2.8$, df = 2, $P = 0.29$). White crappie diets were dominated by *Daphnia* spp. (frequency of occurrence = 96%), but the presence of walleyes in white

Fig. 1. Relationships between catch-per-unit-effort (CPUE = fish per trap net night) of 130- to 199-mm white crappies (*Pomoxis annularis*; CPUE white crappie = $\log_{10}$(CPUE + 1)), mean spring (March through May) elevation (metres above mean sea level (msl)), spring storage ratio (SR = volume at conservation pool/reservoir discharge volume), mean spring temperature (°C), and catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes (*Stizostedion vitreum*; CPUE = $\log_{10}$(CPUE + 1)) in (*a*) Glen Elder, (*b*) Kirwin, (*c*) Webster, and (*d*) Wilson reservoirs, Kansas, during 1985–1999. Symbol size is directly proportional to $\log_{10}$(CPUE + 1) of age-0 walleyes, with large symbols representing high catch rates and small symbols representing low catch rates of age-0 walleyes.



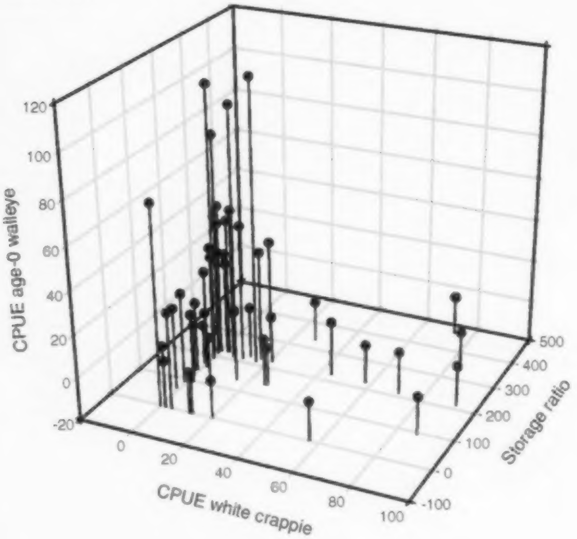
crappie stomachs (frequency of occurrence = 53%) confirmed consumption of walleyes.

Discussion

Knowledge of factors associated with recruitment variability across a variety of systems and regions is important for a complete understanding of walleye ecology and for predicting the response of walleye population dynamics to changes in abiotic conditions (e.g., water-level alterations, elevated thermal regimes) and biotic interactions (e.g., species introductions or losses). Understanding these factors is especially important in reservoirs where species have no evolutionary history with the abiotic conditions and little or no history of co-occurrence with members of reservoir fish assemblages, especially in the southern Great Plains where the highly variable climate results in marginal walleye habitat (e.g., high summer temperatures). Despite differences among aquatic systems (i.e., lotic, lentic, and reservoir) and regions, several generalizations have emerged from the results of previous research and our study.

The most important abiotic factors associated with recruitment of walleyes across their distribution appear to be temperature, wind, and water-level characteristics during the spring. Busch et al. (1975) and Madenjian et al. (1996) found that temperature warming rate during spring was related to walleye recruitment in Lake Erie. Hansen et al. (1998) found that variation in temperature during May partially explained walleye recruitment dynamics in Escanaba Lake, Wisconsin. Although we expected that spring warming rate or variation in temperature would be related to walleye recruitment, only mean temperature was related to catch rates of age-0 walleyes in Kansas reservoirs. Water temperatures are influenced by a variety of factors in addition to air temperature, such as precipitation or reservoir inflow. Thus, our measure of temperature (i.e., air temperature) was probably insensitive to small differences in the rate of warming or variation in water temperatures. For instance, water temperatures in Glen Elder Reservoir during the spring of 1999 were highly variable and exhibited a slow rate of warming compared with 2000 and 2001 (Quist 2002). Although mean air and water temperatures have been known to be highly correlated for Kansas reservoirs (Quist et al. 2002), air temperature failed to display large differences in warming rates or temperature variability. However, air temperatures were about 4°C lower in 1999 relative to 2000 and

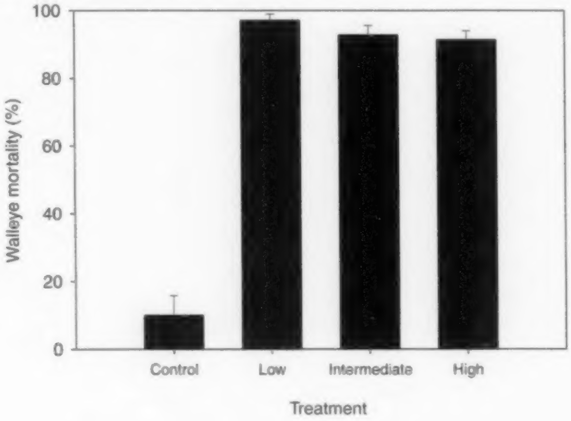
Fig. 2. Relationship between catch-per-unit-effort (CPUE = fish per trap net night) of 130- to 199-mm white crappies (*Pomoxis annularis*; CPUE white crappie = $\log_{10}(\text{CPUE} + 1)$), spring storage ratio (SR = volume at conservation pool/reservoir discharge volume), and catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes (*Stizostedion vitreum*; CPUE = $\log_{10}(\text{CPUE} + 1)$) in all four Kansas reservoirs during 1985–1999.



2001, suggesting that our surrogate measure of water temperature may not only reflect lower mean water temperatures, but also slower warming rates or higher variability. Regardless, weak walleye year classes were produced during years with low mean air temperatures during the spring, which may have caused extended incubation times resulting in prolonged risk of egg predation, increased exposure to the effects of wind (Houde 1969; Busch et al. 1975), or reduced growth and survival of larvae (Colby et al. 1979).

In addition to climatic factors, we found that walleye recruitment was related to low spring elevations and high spring storage ratios. Willis and Stephen (1987) found a similar relationship between walleye recruitment and storage ratio in several Kansas reservoirs and suggested that loss of walleyes during high discharge events (i.e., low storage ratio) was the dominant mechanism. Although direct loss of walleyes may be an important factor during extremely high discharge events, our study suggests that strong walleye year classes were only produced during years with both high storage ratios and low elevations. During years with low elevations and high storage ratios, we observed relatively small (i.e., ≤1.5 m) increases in water levels. Chevalier (1977) reported similar results, where small increases in water level (i.e., 1–2 m) were important for recruitment of walleyes in Rainy Lake, Minnesota and Ontario. Water-level increases less than 1 m were related to high recruitment of walleyes in lakes from Voyageurs National Park, Minnesota (Kallemeyn 1987). Similar results have been reported for Missouri River reservoirs, where small, gradual increases in reservoir elevation were important for walleye recruitment (Nelson and Walburg 1977). The specific mechanisms responsible for the trends observed in our study are unknown, but previous research suggests that walleye recruitment may be enhanced by small increases in water levels by either increased quantity and quality of spawning habitat or indirectly by increased production of prey species (Chevalier 1977; Nelson and Walburg 1977).

Fig. 3. Mean walleye mortality (%) owing to predation of juvenile white crappies (*Pomoxis annularis*) at three zooplankton treatments. Error bars represent 1 SE. Walleye mortality in the low, intermediate, and high zooplankton treatments was not significantly different ($P = 0.29$).



Walleye recruitment is undoubtedly influenced by abiotic constraints across their distribution; however, interactions with other members of the fish community may have an overriding influence on walleye recruitment dynamics. Competition and cannibalism have been shown to influence walleye recruitment in a variety of systems (Colby et al. 1979). Interspecific predation by endemic species such as smallmouth bass (*Micropterus dolomieu*; Johnson and Hale 1977), yellow perch (*Perca flavescens*; Mion et al. 1998), and sauger (*Stizostedion canadense*; Swenson and Smith 1976) may also influence walleye recruitment in natural systems. If predation by endemic species can influence recruitment of walleyes in natural systems, we would expect biotic interactions to be as important in systems with introduced species. In our study, the abundance of adult walleyes, white bass, and gizzard shad were unrelated to walleye recruitment. Contrary to many other systems (e.g., Forney 1980), cannibalism does not appear to influence recruitment dynamics of walleyes. Quist et al. (2002) examined the stomach contents of 247 walleyes from Glen Elder Reservoir and no evidence of cannibalism was observed. Although gizzard shad may negatively influence recruitment of piscivores (Stein et al. 1995), gizzard shad abundance was not a significant variable in any of our models. However, recent investigations suggest that low water temperatures in Glen Elder Reservoir mediate interactions between larval gizzard shad and walleyes, where low water temperatures resulted in poor growth of larval walleyes, an inability to switch to piscivory, and poor recruitment (Quist 2002). Abundance of white crappies was the only biotic variable that was related to walleye recruitment in our study.

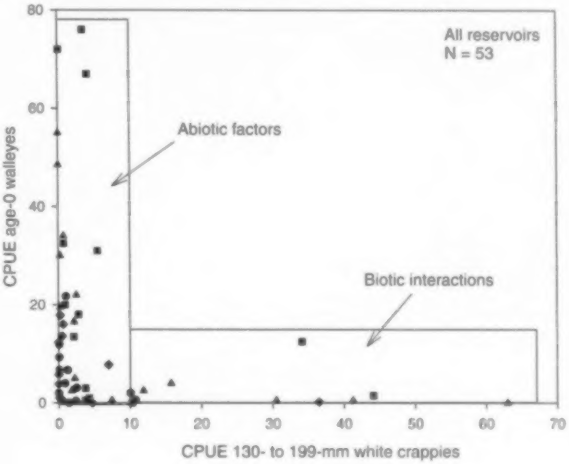
An important theory regarding the native distribution of percids in North America states that interactions with centrarchids restricted their success in southern latitudes (Collette et al. 1977). Several studies support this hypothesis of introductions of centrarchids to systems with native walleye populations (Schiavone 1985) or introductions of walleyes to centrarchid-dominated systems (Santucci and Wahl 1993) resulting in poor walleye recruitment. The results of our empirical analysis and mesocosm experiment also support this hypothesis.

Adult white crappies potentially limit recruitment of larval fishes in some systems (Kim and DeVries 2001), but the influence of juvenile white crappies on larval fish mortality has not been previously investigated. Juvenile white crappies prey almost exclusively on zooplankton until they reach a length of about 170 mm (O'Brien et al. 1986), but smaller white crappies will consume larger prey items when available. For example, Wright and O'Brien (1982) found that the reactive distance of white crappies increased linearly with prey size (i.e., larval *Chaoborus*) and that movement of prey doubled the distance that prey could be detected. White crappies also have a saltatory search strategy (i.e., alternating swim–search behavior) that can be modified when prey are located to increase consumption rates (e.g., reduce time between searches; O'Brien et al. 1986). If larval fishes have a patchy distribution owing to factors such as wind-generated water currents or the indirect effect of prey distributions, predation rates may be high given the behavior and size of larval fishes and the feeding ecology of juvenile white crappies (Wright and O'Brien 1982; O'Brien et al. 1986).

Although the mesocosms used in this study were large enough to avoid small-container effects (de Lafontaine and Leggett 1987), experiments were conducted using larval densities (2.3 walleyes·m^{-3}) much higher than those observed in the field (i.e., <1.0 walleyes·m^{-3}; Quist 2002). Despite differences in density, the ratio of *Daphnia* spp. to larval walleyes in the high zooplankton treatment was equal to or higher than that observed in the field. Thus, even though white crappies had to locate walleyes among the same (or higher) number of zooplankton, mortality still exceeded 90% over a short time period.

Abiotic and biotic factors were associated with walleye recruitment in Kansas reservoirs, but the results of our empirical and experimental analyses suggest that biotic interactions can have an overriding influence on walleye recruitment dynamics. For example, strong walleye year classes should have been produced when abiotic characteristics were suitable in each reservoir, but walleye recruitment was limited when juvenile white crappies were abundant. Therefore, we propose a biotic–abiotic confining hypothesis (BACH) to explain the role of abiotic and biotic mechanisms on walleye recruitment in Kansas reservoirs. During years with low white crappie abundance, walleye recruitment is highly variable and is likely confined by abiotic factors (Fig. 4). However, when juvenile white crappie abundance reaches some threshold value, which will vary by reservoir, walleye recruitment is low. The influence of white crappies on walleye recruitment is probably direct, as suggested by our experimental results. Furthermore, if white crappies did not have an influence on walleyes, we would expect to observe high variability in walleye recruitment at all levels of white crappie abundance, but this has not occurred in any reservoir over the past 15 years.

Fig. 4. Relationship between catch-per-unit-effort (CPUE = fish per gill net complement night) of age-0 walleyes (*Stizostedion vitreum*) and CPUE (CPUE = fish per trap net night) of 130- to 199-mm white crappies (*Pomoxis annularis*) in four Kansas reservoirs (Glen Elder, ●; Kirwin, ■; Webster, ▲; and Wilson, ◆) during 1985–1999. Based on this relationship, we propose a biotic–abiotic confining hypothesis (BACH) to explain the role of biotic interactions and abiotic conditions on walleye recruitment dynamics in Kansas reservoirs.



In conclusion, the results of this study provide important information on factors influencing recruitment dynamics of walleyes in reservoir ecosystems and suggest that spring temperatures and water levels are important for walleyes regardless of the ecosystem or region. The specific mechanisms for the abiotic relationships are unknown for Kansas reservoirs but are probably similar to systems in northern latitudes. This study also illustrates the potential influence of biotic interactions on walleye recruitment in reservoirs, and the BACH provides a model for conceptualizing factors influencing walleye recruitment. Although our analysis was limited to Kansas reservoirs, similar factors probably influence walleye recruitment in other Great Plains reservoirs because of similarities in reservoir fish communities and abiotic conditions (e.g., water-level fluctuations, thermal regimes) throughout the southern Great Plains region.

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Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho

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Abstract: Metapopulation dynamics have emerged as a key consideration in conservation planning for salmonid fishes. Implicit to many models of spatially structured populations is a degree of synchrony, or correlation, among populations. We used a spatially and temporally extensive database of chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho to examine patterns in synchrony as these fish underwent a sixfold decrease in abundance. Our results suggested that populations became strongly synchronous as abundances decreased and that the range, or diversity of correlations, exhibited among populations also decreased. These changes indicate that the likelihood of simultaneous extirpations has increased, which could have long-term detrimental consequences for metapopulation persistence. Implications for management are that the resilience of many metapopulations to large-scale disturbance and anthropogenic suppression may not depend solely on attempts to maintain large and productive component populations, but also on efforts to desynchronize populations that have become strongly correlated. Such efforts could entail promoting the existence of a broad distribution and diversity of habitats that support a wide array of life-history forms and ensuring that some habitats are sufficiently spatially disjunct so that risks from catastrophic stochastic events are minimized.

Résumé : La dynamique des métapopulations est devenue un élément primordial de la planification de la conservation des poissons salmonidés. Plusieurs des modèles de population à structure spatiale supposent l'existence d'un degré de synchronisation ou de corrélation entre les populations. Une importante banque de données, tant spatiales que temporelles, de dénombrements de saumons quinnat (*Oncorhynchus tshawytscha*) sur les frayères dans une région sauvage du centre de l'Idaho nous a permis d'examiner la synchronisation au moment où ces poissons subissaient un déclin de leur abondance par un facteur de 6. Nos résultats montrent que les populations se synchronisent fortement à mesure que leur abondance diminue et que l'étendue ou la diversité des corrélations entre les populations décroît aussi. Ces changements indiquent un accroissement de la vraisemblance d'une extirpation simultanée, ce qui pourrait avoir des conséquences néfastes sur la survie de la métapopulation. Il y a aussi des implications pour la gestion : la résilience de plusieurs métapopulations aux bouleversements à grande échelle et à l'extermination par l'activité humaine peut ne pas dépendre uniquement d'efforts pour maintenir des populations constitutives importantes et productives, mais aussi d'efforts pour désynchroniser les populations qui sont en forte corrélation. On pourrait penser au développement d'une large répartition et diversité d'habitats où prévaudrait une gamme étendue de types de cycles biologiques et à la précaution que certains habitats soient suffisant éloignés les uns des autres pour que les risques engendrés par des événements catastrophiques stochastiques soient minimisés.

[Traduit par la Rédaction]

Introduction

The Columbia River Basin once harbored abundant populations of spring and summer chinook salmon (*Oncorhynchus tshawytscha*; Lichatowich 1999), but populations of these fish have declined precipitously over the last century. Thurow et al. (2000) estimated that spring and summer chinook salmon in the interior Columbia River Basin presently occur in only 21% of the historical range. Many remaining stocks persist at dangerously low levels (Nehlsen et al. 1991; Huntington et al. 1996), which has prompted federal protection under the U.S. Endangered Species Act (ESA). Whereas much of the recent debate regarding salmon conservation efforts has focused on the relative importance of various factors, including dams, ocean productivity, hatcheries, and habitat alterations (Ruckleshaus et al. 2002), there is little

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debate that populations have declined. Although these declines have obvious implications for the persistence of individual populations, repercussions may also occur with regards to how populations interact across larger spatial and temporal scales.

The dynamics of multiple, potentially interacting local populations, often described as "metapopulations" (Hanksi 1999), has emerged as a key consideration in conservation planning for salmonid fishes. Although understanding metapopulation dynamics in salmonid fishes is limited (Rieman and Dunham 2000), all models of spatially structured populations are characterized by some degree of synchrony, or correlation, among populations (Harrison and Taylor 1996). A low level of correlation is often regarded as beneficial because habitats vacated by local extirpations can be recolonized by dispersal from nearby populations that were fluctuating out of phase (Sutcliffe et al. 1997). Conversely, a high level of correlation among populations can result in simultaneous extirpations when abundances are low and is predicted to decrease the probability of metapopulation persistence (Heino et al. 1997). Many aspects of reserve design and effective conservation thus hinge on understanding the level of synchrony that exists among local populations (e.g., Pickett and Thompson 1978; Moyle and Sato 1991; McElhany et al. 2000).

Studies on a wide range of animal taxa have addressed the topic of spatial synchrony (see reviews by Bjornstad et al. (1999) and Koenig (1999)). Almost invariably, these studies document a negative relationship between correlation in a population parameter — typically abundance — and the geographic distance separating populations. At short distances, dispersal of individuals between populations is believed to be a primary synchronizing factor (Sutcliffe et al. 1997; Ranta et al. 1997), but correlated environments also synchronize population dynamics and may act over greater distances (Heino et al. 1997). Local factors, such as density dependence, heterogeneities in habitats, or small-scale stochastic events, can override or decrease the importance of synchronizing agents and result in population asynchronies (Haydon and Steen 1997; Kendall et al. 2000).

The life histories of salmonid fishes provide ample opportunity for a complexity of factors to interact and affect spatial and temporal correlation of local populations. This is particularly true for salmon that migrate long distances and use a broad diversity of habitats during their life cycle. Salmon often spawn in headwater stream habitats, where local environmental factors can have important influences (Gomi et al. 2002), possibly affecting the synchrony of dynamics among local breeding areas. Other key features of salmon life histories are migration and ocean residence, which may lead to changes in synchrony, dependant on the timing, specific location, and types of activities that occur within these habitats (Peterman et al. 1998; Pyper et al. 2001).

Spatial synchrony studies are just beginning to describe patterns and their potential causes for salmonid fishes. Rieman and McIntyre (1996) noted weak but significant correlations among bull trout (*Salvelinus confluentus*) populations across northern Idaho and northwest Montana. Salmon recovery efforts have used synchrony analysis in attempts to identify unique or independent populations with mixed results (Currens et al. 2001). Other studies have used patterns in synchrony to make inferences about the spatial scales at which environmental controls act on individual stocks in efforts to develop improved management policies (Pyper et al. 1999; Botsford and Paulsen 2000; Pyper et al. 2001). In most cases, however, previous studies have been conducted at spatial scales of regional extent, where questions pertaining to metapopulation dynamics are largely negated. In this paper, we focus on a population assemblage of chinook salmon within a wilderness area drained by the Middle Fork of the Salmon River (MFSR) in central Idaho. Within this area, a database that encompasses 45 years of redd counts from multiple sites within close proximity allows us to ask questions not only about spatial patterns in correlations, but also about the temporal stability of these patterns, and to do so at a scale relevant to metapopulation considerations.

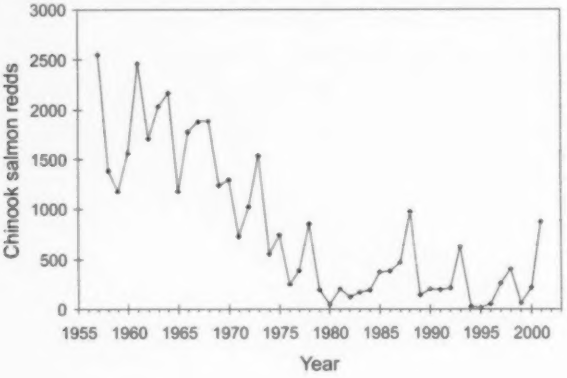
Materials and methods

Sample site

Chinook salmon populations that occur within the MFSR are composed of wild, indigenous fish. Redd counts conducted by the Idaho Department of Fish and Game (IDFG) suggest that these populations have declined to less than 20% of their abundance in the 1950s (Fig. 1; Brown 2002). These populations have been afforded federal protection since 1992, when all species of Snake River salmon were ESA listed. Populations within the MFSR are referred to as "spring/summer" chinook salmon based on the timing of adult migration past Bonneville Dam in the lower Columbia River (Matthews and Waples 1991). Chinook salmon enter the MFSR drainage in early summer, migrate to natal areas, and stage in pools before spawning. Eggs are deposited and fertilized in nests or redds from late July to mid-September. Embryos incubate in the gravel and emerge as fry the following spring. Although variable, juveniles typically rear in natal areas for 1 year before migrating seaward in the spring (Bjornn 1971). Migrating juveniles and returning adults must navigate eight hydroelectric dams on the lower Snake and Columbia rivers. Adults spend 1–3 years in the ocean, with the proportion of 1-, 2-, and 3-ocean fish varying across years and streams (Kiefer et al. 2002). Other salmonids that occur within the MFSR include bull trout, westslope cutthroat trout (*Oncorhynchus clarki lewisi*), mountain whitefish (*Prosopium williamsoni*), rainbow trout (resident forms and migratory steelhead; *Oncorhynchus mykiss*), and brook trout (*Salvelinus fontinalis*; Thurow 1985). Other species of salmonids are stocked in headwater lakes within the basin but are generally not found within areas used by chinook salmon (Pilliod and Peterson 2001).

The MFSR drains 7330 km^2 of forested and steeply mountainous terrain in central Idaho that ranges in elevation from 1550 to 3150 m (Fig. 2). Major tributaries along the 171 km length of the MFSR provide spawning habitat for chinook salmon. Spawning also occurs within portions of the mainstem river but has been uncommon in recent years (Thurow 2000). Most lands within the MFSR (>95%) are administered by the U.S. Forest Service, and the area was managed as a primitive area from 1930 to 1980 before receiving permanent protection as part of the Frank Church River of No Return Wilderness in 1980. As a result, road and trail densities are low and most streams exist in rela-

Fig. 1. Aggregated time series of chinook salmon (*Oncorhynchus tshawytscha*) redd counts for the Middle Fork Salmon River basin. Data are from annual Idaho Department of Fish and Game surveys of chinook salmon spawning index areas (Brown 2002).



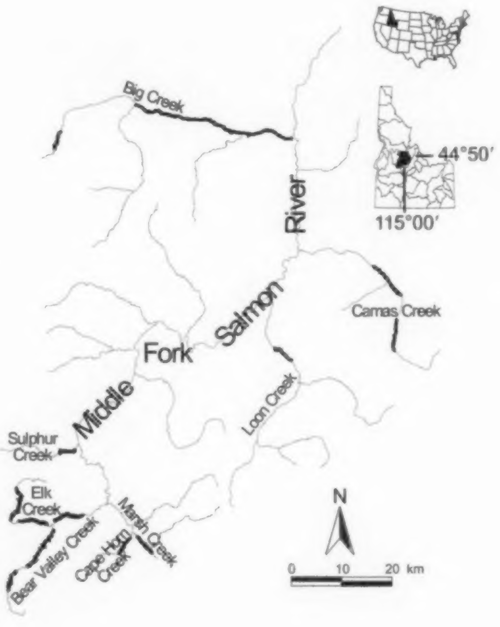
tively pristine condition. Some areas continue to recover from the effects of past grazing or mining, but cessation of many of these activities has occurred since wilderness designation and ESA listing. Natural disturbances from fires, hillslope movements, and floods persist, and these processes help maintain the dynamic mosaic of stream habitats that exist within the MFSR (e.g., Miller et al. 2003; Nakamura et al. 2000). Most precipitation occurs as snowfall, and stream hydrographs are dominated by snowmelt with peak runoff in June, followed by low flows from late July through March.

Streams flow through wide, U-shaped valleys in the upper portion of the MFSR drainage, but elsewhere valleys are typically narrow and V-shaped. Land surfaces consist primarily of colluvium overlain by thin soils, but bedrock outcrops are not uncommon. Geology is varied, and Cretaceous-aged calc-alkaline intrusive materials of the Idaho Batholith occur across the southern half of the drainage, except where overlain by Quaternary alluvium and Pleistocene glacial drift (primarily in the Bear Valley Creek and Marsh Creek subbasins; Bond and Wood 1978). Streams in east-central and west-central portions of the drainage flow over felsic pyroclasts of the Challis Volcanics. The northern part of the drainage is a heterogeneous mix of several geologic formations (Bond and Wood 1978). Vegetation varies with elevation and aspect. Sagebrush (*Artemsia* spp.), grasses, and forbs are common at lower elevations and on southern slopes, whereas conifers predominate at higher elevations and on northern slopes.

Data collection

Data were derived from annual spawning ground surveys conducted by IDFG personnel on MFSR spawning tributaries. In recent years, some of these counts have been conducted by Rocky Mountain Research Station personnel. Salmon redds were counted by individual observers during a single pass along a stream transect and were timed to occur at or soon after the peak of spawning activity. The same biologist often conducted counts for the same set of transects during many consecutive years, although the length of the data record has required that multiple individuals contribute to each time series. Redd counts have been conducted on foot and by using aircraft — either small airplanes or helicopters. Foot surveys are generally used in accessible portions of the drainage, whereas aircraft are often used to sample remote areas. Redds have been counted with varying degrees of consistency at numerous areas on MFSR streams since 1952, but geographic boundaries were not standardized until 1957 (Hassemer 1993). For inclusion in this study, we selected data from 13 sample transects that were distributed across the MFSR and which had been sampled frequently within consistent geographic boundaries since 1957 (Table 1; Fig. 2). The prevalence of errors in this data set is unknown, but given the long time series and dramatic changes in populations that have occurred, we judged the data to be valuable for analyzing patterns and developing initial hypotheses.

Fig. 2. Stream network in the Middle Fork Salmon River. Dark bars indicate Idaho Department of Fish and Game sampling transects used in this study.



Data analysis

The temporal extent of the redd counts made it possible to examine the consistency of spatial patterns across time and population sizes. We stratified the 13 series of redd counts into two periods — a high-abundance period from 1957 to 1973 (mean = 1624) and a low-abundance period from 1979 to 2000 (mean = 252). Analyses were completed on raw- and detrended-redd numbers. Detrending was done using two methods — interannual differencing and linear regression. Annual differences were calculated as $\log_e(N_i/N_i - 1)$, where N_i was the redd count in year *i*. Differencing provided a measure of the instantaneous rate of population change and was independent of population size. In the regression-based method, individual series of redd counts were regressed against sample year within each stratum and subsequent analyses

Table 1. Summary of chinook salmon redd counts for three periods at 13 sampling transects in the Middle Fork Salmon River.

	Entire record (1957–2001)			High-abundance period (1957–1973)			Low-abundance period (1979–2000)		
Sampling transect	Years sampled	Mean redd count	CV	Years sampled	Mean redd count	CV	Years sampled	Mean redd count	CV
Upper Big Creek	44	68	1.06	17	120	0.72	22	28	0.94
Lower Big Creek	30	85	1.43	14	167	0.83	14	9	0.77
Lower Camas Creek	41	59	0.96	14	113	0.43	21	15	0.96
Upper Camas Creek	31	40	1.15	11	86	0.56	14	6	1.58
Loon Creek	33	37	1.06	11	75	0.52	16	9	0.85
Sulphur Creek	36	38	1.18	8	107	0.33	22	13	1.19
Marsh Creek	45	109	0.89	17	206	0.39	22	38	0.94
Cape Horn Creek	45	39	0.97	17	66	0.58	22	15	1.11
Lower Bear Valley Creek	45	92	0.89	17	176	0.38	22	31	0.98
Middle Bear Valley Creek	45	105	1.05	17	216	0.48	22	29	0.89
Upper Bear Valley Creek	45	15	1.12	17	30	0.63	22	6	1.22
Lower Elk Creek	45	87	0.94	17	176	0.35	22	25	0.99
Upper Elk Creek	45	109	0.94	17	207	0.40	22	42	1.37
Average	41	68	1.05	15	134	0.51	20	21	1.06

Note: Coefficient of variation (CV) = standard deviation/mean.

were conducted on the residuals. Detrending minimized the possibility of spurious correlations among redd counts as a result of long-term, linear trends in redd numbers and focused the analysis on local population dynamics (Koenig 1999).

We quantified synchrony by calculating Pearson correlations among all pairwise combinations of redd counts and detrended redd counts within each stratum. Because temporal autocorrelation within a time series can result in liberal estimates of significance (Type I statistical error) for interseries correlations (Botsford and Paulsen 2000), statistical significance was determined by comparing the observed correlations with reference distributions that were obtained by recalculating correlations after each of 1000 randomizations of a time series (Howell 2002). Within each stratum, we tested whether the mean correlation equaled zero and whether a difference in mean correlations occurred across strata. Statistical significance was determined using bootstrap methods because only $(C - 1 + C - 2)$ pairwise correlations of all possible pairwise correlations $(C(C - 1))/2)$ can be calculated independently (C is the number of time series considered; Ranta et al. 1997). For each test, 95 and 99% confidence intervals were constructed using the SE derived from 1000 bootstrap samples.

The relationship between population synchrony and distance was described for each stratum by regressing correlations against the stream distance that separated the midpoints of sample transects. Stream distances were measured from a 1:100 000 scale hydrology layer in a geographic information system (GIS). Significance levels for slope parameters were calculated using a randomization approach to avoid the problems with nonindependence discussed above (Legendre and Legendre 1998). Difference in the slopes of the relationships was tested by calculating the ratio of the slope difference to the SE of the slope difference and comparing this value with a t distribution (Zar 1996).

To provide a temporally detailed view of changes in population synchrony, we calculated correlations for an 8-year sampling frame that was advanced at 1-year increments through each pair of redd count time series. Because data were collected sporadically at some transects, these calculations were made only for pairs of transects that had been sampled concurrently for more than 20 years.

Results

Chinook salmon redds were counted at the 13 sample transects included in this study from 31 to 45 years (Table 1). The number of sample years in high- and low-abundance periods ranged from 8 to 17 (mean = 15) and 14 to 22 (mean = 20), respectively. Mean redd counts during the early period of high abundance ranged from 30 to 216 redds and averaged 134, whereas mean redd counts during the subsequent low abundance period ranged from 6 to 42 and averaged 21. Coefficients of variation during the low-abundance period were larger than during the high-abundance period at 12 of 13 transects.

Patterns in synchrony for raw redd counts and both forms of detrended redd counts were virtually identical, so only results based on detrended regression residuals are presented. Significant correlations between redd counts were common during both periods (Table 2). The mean correlation for each period differed significantly from zero (high abundance $r = 0.34$, $p < 0.01$; low abundance $r = 0.50$, $p < 0.01$), as did the difference between the two periods ($d = 0.16$, $p < 0.01$), suggesting that the overall level of synchrony increased as population sizes decreased. Corroboration of this trend was provided by the number of significant correlations within each period. During high abundance, 23 of 78 correlations were significant at $\alpha = 0.05$, but this number increased to 42 of 78 correlations during the low-abundance period. Significant correlations during the high-abundance period were most common within the geographically proximate transects located in the upstream portion of the MFSR, and significant correlations became virtually ubiquitous in this area at lower escapements (27 of 28 possible correlations). Outside the

Table 2. Correlations among detrended redd count residuals at 13 transects in the Middle Fork Salmon River for two abundance periods.

Transect	Upper Big Creek	Lower Big Creek	Lower Camas Creek	Upper Camas Creek	Loon Creek	Sulphur Creek	Marsh Creek	Cape Horn Creek	Lower Bear Valley Creek	Lower Elk Creek	Upper Elk Creek	Middle Bear Valley Creek	Upper Bear Valley Creek
Upper Big Creek	—	0.15	0.18	–0.08	0.29	0.63	0.80	0.73	0.81	0.67	0.75	0.81	0.75
Lower Big Creek	0.01	—	0.10	0.15	–0.07	–0.03	0.06	–0.02	0.41	–0.01	0.10	0.31	0.17
Lower Camas Creek	0.24	–0.05	—	0.28	0.50	–0.02	0.34	0.35	0.28	0.35	0.41	0.32	0.46
Upper Camas Creek	0.32	0.07	0.79	—	0.49	0.14	0.03	0.64	0.32	0.51	0.52	0.25	0.43
Loon Creek	0.02	0.17	0.59	0.52	—	0.18	0.57	0.70	0.33	0.51	0.65	0.48	0.47
Sulphur Creek	0.39	–0.27	0.32	0.24	0.17	—	0.51	0.61	0.56	0.54	0.50	0.49	0.47
Marsh Creek	0.24	0.04	0.56	0.73	0.24	0.22	—	0.62	0.84	0.75	0.74	0.75	0.68
Cape Horn Creek	0.26	–0.31	0.36	0.21	0.25	–0.06	0.64	—	0.73	0.88	0.87	0.80	0.79
Lower Bear Valley Creek	0.64	–0.37	0.07	0.24	–0.42	0.41	0.44	0.23	—	0.76	0.86	0.83	0.83
Lower Elk Creek	0.44	–0.29	0.72	0.65	0.27	0.64	0.59	0.53	0.47	—	0.92	0.82	0.77
Upper Elk Creek	0.50	–0.02	0.42	0.47	–0.05	0.33	0.48	0.37	0.46	0.76	—	0.88	0.85
Middle Bear Valley Creek	0.32	0.20	0.78	0.66	0.34	0.68	0.53	0.50	0.20	0.74	0.54	—	0.91
Upper Bear Valley Creek	0.14	–0.27	0.63	0.41	0.31	0.50	0.70	0.66	0.36	0.68	0.38	0.59	—

Note: Correlations below the diagonal are for the high abundance period from 1957 to 1973; correlations above the diagonal are for the low abundance period from 1979 to 2000. Correlations with significance levels ≤ 0.05 are shaded; correlations with significance levels ≤ 0.01 are solid black. Box encompasses sites within the upstream portion of the Middle Fork Salmon River.

upper MFSR, redd counts in Loon Creek and upper Big Creek became more synchronous with other areas, whereas lower Camas Creek became less synchronous.

Regressions of correlational strength on distance had negative slopes that were different from zero for both periods (high abundance $b_1 = -0.0012$, $p < 0.01$; low abundance $b_1 = -0.0014$, $p < 0.01$; Fig. 3), suggesting that redd count synchronies were stronger among proximal transects than among distant transects. Slopes of the two regression lines were not different ($t = 0.35$, $p = 0.73$), but as would be expected given the difference in mean correlations, the Y intercept was significantly larger for the low-abundance period ($t = 2.34$, $p = 0.02$).

The moving window analysis suggested that the mean correlation among redd count time series steadily increased from an initial value of 0.23 to the most recent value of 0.88 as population abundance decreased (Fig. 4). Coincident with this increase, the range of associated interseries correlations has narrowed. Whereas correlations early in the time series were negative, near zero, or positive, correlations later in the series were usually strongly positive. Also noteworthy is that interseries correlations varied considerably during the time series — often exhibiting large changes in magnitude over the span of a few years. Part of this variability could be attributable to sampling variation given the relatively short 8-year length of the sampling frame, but similar patterns were observed when sampling frame lengths were extended to 13 years.

Discussion

Our results provide insight into how a group of wild, indigenous chinook salmon populations in a relatively pristine setting have functioned during the last half century. The picture that emerges is one of a system that has been highly dynamic in both space and time. Coincident with sometimes dramatic short-term fluctuations among populations, overall abundance has undergone a sixfold decrease, correlations among populations have increased, and the range of interseries correlations has narrowed. Combined, these patterns are indicative of a system that has transitioned from a high level of stability and resilience to a state in which these qualities appear greatly reduced. The diversity and low level of synchrony once manifest within this system appear to have provided the capacity necessary to maintain some level of functionality while undergoing severe population declines. At the present time, however, further capacity for change seems limited and scenarios involving multiple simultaneous extirpations could become reality and have long-term detrimental consequences for metapopulation persistence.

The diverse life history of chinook salmon includes occupation of several distinct environments and opens the possibilities to a range of hypotheses that may explain the dramatic changes in correlations among these populations. One possibility may be the decreased availability of nutrients in freshwater rearing environments that has undoubtedly resulted from massive declines in adult carcasses. Previous studies suggest that salmon carcasses, either through direct consumption (Chaloner and Wipfli 2002) or through the release of inorganic nitrogen and phosphorus (Schuldt and Hershey 1995), may increase productivity of lower trophic levels and

Fig. 3. Trends in correlations among detrended redd counts relative to stream distance for all pairwise combinations of Idaho Department of Fish and Game transects during two abundance periods. Open circles are correlations exhibited during the high-abundance period (shaded trend line); solid squares are correlations exhibited during the low-abundance period (solid trend line).

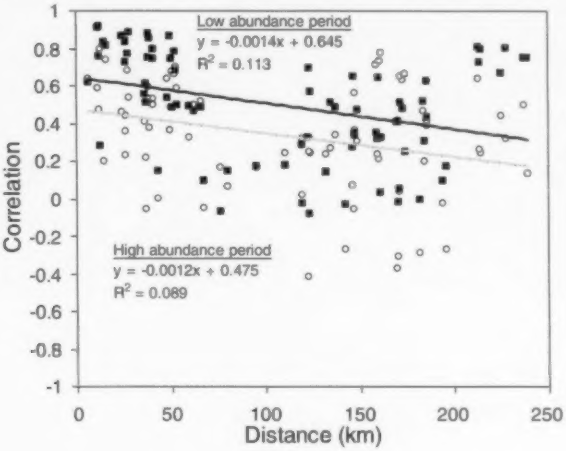
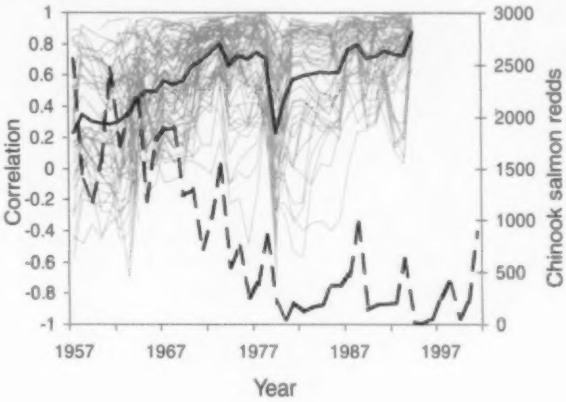


Fig. 4. Temporal trends in correlations among all pairwise combinations of redd counts at Idaho Department of Fish and Game transects. Correlations were calculated based on an 8-year sampling frame that was advanced at 1-year increments through paired time series. Shaded lines represent interseries correlations; heavy solid line represents the mean correlation; heavy broken line represents the aggregated time series of chinook salmon redd counts from Idaho Department of Fish and Game trend sites in the Middle Fork Salmon River.



the growth rates and size of fish (Mundie et al. 1991). Although little evidence exists for decreases in survival or productivity of MFSR stocks during freshwater rearing (Petrosky et al. 2001), other more subtle changes are possible. For example, the timing of migration and even the expression of some life histories appear to be partially dependent on juvenile growth (Healy and Heard 1984). Changes in growth, therefore, could have altered the developmental trajectories and environments experienced by a fish, and as carcasses decreased within the MFSR, juvenile growth and the range of available life-history options may have simply become restricted (e.g., Gende et al. 2002).

Another possibility is that changes in synchrony are related to decreases in the importance of density-dependent regulatory mechanisms. Stock–recruitment theory suggests that density dependence decreases to zero as stock size decreases, whereas the relative importance of density-independent mortality factors increases (Hilborn and Walters 1992). As a result, the buffering effect that density dependence provides individual populations against stochastic events and that also helps maintain asynchrony among populations (Kendall et al. 2000) is minimized, and populations could become correlated in response to stronger density-independent control. Although a density-dependent mechanism could exert influence during several life stages, researchers working with both freshwater (Rieman and McIntyre 1996) and anadromous fishes (Peterman et al. 1998) have argued that patterns in synchrony are largely determined before establishment of residence in lentic or oceanic habitats, which may only serve to enhance preexisting patterns, given the relative homogeneity of these habitats. Rieman and McIntyre (1996) predicate their argument upon the establishment of relative year-class strength early in life, whereas Peterman et al. (1998) suggest that only minor changes in synchrony occur after juveniles emigrate from rearing habitats. If this scenario is applicable to the MFSR, current conditions probably differ from historical conditions when population responses were metered by the degree of density dependence. Under historical conditions, similar environmental stimuli, acting upon a range of population abundances, would have resulted in differential responses and may have generated asynchronous dynamics.

Land management activities and the suppression of natural disturbance regimes have resulted in the homogenization of stream habitats in many landscapes (Bisson et al. 1992; McIntosh et al. 2000). As the diversity of available rearing habitats is diminished, populations increasingly occur in similar habitats and experience similar environments. This trend could be an important synchronizing agent in many managed areas but seems unlikely in the wilderness setting in which our study was conducted. Minimal anthropogenic effects and a geographic size that facilitates the existence of natural disturbance processes ensure the continual generation and maintenance of a diversity of stream habitats. Although the array of stream habitats available to fish under such conditions may constantly be changing (Bisson et al. 1997), it is doubtful that a sustained unidirectional shift in the physical characteristics of stream habitats could occur over a time span sufficient to evoke a systemic response in population synchrony. Additionally, the time scale of such changes is likely to greatly exceed the length of the time series considered here (Wolman and Gerson 1978).

Factors outside the MFSR may have contributed to the pattern that we observed. The hydrosystem on the lower Snake and Columbia rivers was constructed coincident with changes that occurred in synchrony. Recent data suggest that the timing of smolt migration through the hydrosystem strongly affects juvenile survival and adult returns (J. Williams, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112, unpublished data). If temporal patterns in smolt migrations and hydrosystem survival are consistent among years, the hydrosystem could effectively act as a filter that selects for particular life histories, ultimately decreasing the range of viable life-history options.

Marine conditions are also a strong determinant of survival in anadromous salmonids (Mantua et al. 1997; Hare et al. 1999), and patterns in correlations have been documented among anadromous fish stocks in many coastal regions (Peterman et al. 1998; Pyper et al. 1999). To date, however, these patterns have emerged only at large spatial scales (e.g., coastal regions of the northeast Pacific ocean; Pyper et al. 2001; Mueter et al. 2002*a*), and for the marine environment to have become a stronger synchronizing factor implies either that the ocean has become more homogenous relative to the scales at which fish from the MFSR use it or that distributional patterns have changed and fish are now using more similar environments than previously. These explanations seem unsatisfactory, however, given that patchiness in many of the marine variables that affect ocean survival emerges only at geographic scales exceeding hundreds of thousands of square kilometres (Mueter et al. 2002*b*). Instead, rather than changes in synchrony occurring within out-of-basin environments, these environments may have indirectly precipitated the synchronization of MFSR populations by decreasing out-of-basin survival rates (Mantua et al. 1997; Deriso et al. 2001; Petrosky et al. 2001), which decreased numbers of returning adults and thereby facilitated mechanisms that operate during freshwater rearing.

Another possibility is that redd count errors have decreased through time, thus giving the appearance that an increase in correlation has occurred. This scenario implies either that improved sampling protocols and observer competences have resulted in markedly improved redd counts or that population declines and lower associated redd densities have led to fewer counting errors. The former explanation seems less likely given that Hassemer (1993) reviewed the IDFG redd count database and revised its content for consistency in the early 1990s. The data used in this study were a subset of this database that met even stricter requirements regarding sampling consistency. Additionally, although the temporal extent of the redd count time series used in this study has required contributions by numerous individuals, most of the counts have been conducted by highly experienced biologists who have surveyed the same transects for many consecutive years, even decades. Potentially more problematic is the possibility that error rates were greater when population levels, redd densities, and the amount of superimposition were higher. Unpublished data from research designed to assess the accuracy of chinook salmon redd counts suggests that miscounts do occur more frequently at redd clusters than at individual redds (R. Thurow, personal observation). However, even in reaches in which clustering and superimposition are common, reach-scale error rates appear to be relatively small, especially in comparison with other salmonid species like bull trout (Dunham et al. 2001). As a result, even if changes in redd count accuracy have occurred, this mechanism appears incapable of accounting for the entirety of the increase in synchrony that we observed.

Temporal instability in biological systems has implications for fisheries research and population assessments. Several studies of metapopulation dynamics in salmonids have relied on cross-sectional data sets collected after populations had declined substantially (Rieman and McIntyre 1995; Dunham et al. 1997; Dunham and Rieman 1999). As our results suggest, present patterns may not be indicative of past performance. Additional evidence or longer time series may be needed before definitive conclusions can be drawn about many systems (Clinchy et al. 2002). Also potentially problematic is the use of redd counts conducted within a subset of available habitat. Depending on the amount of correlation between sampled and unsampled areas, as well as the temporal stability of these correlations, redd counts may or may not provide accurate assessment of population trends. Remedies for this problem might include surveying the entirety of an area, assessing patterns of synchrony in existing redd count data, or improving sampling designs (e.g., Larson et al. 2001).

Negative relationships were observed between population synchrony and distance during both high- and low-abundance periods, suggesting that proximal populations performed more similarly than distant populations. Rieman and McIntyre (1996) documented a similar pattern for bull trout and concluded that where correlations were weak, the existence of strong proximal populations should be promoted as a means to facilitate the exchange of individuals. This advice remains sound, but caution must be exercised in systems characterized by high levels of synchrony. In these situations, benefits of maintaining populations in close proximity must be balanced with risks of simultaneous extirpations that could threaten the regional persistence of a species, especially in regions characterized by landscape conditions that are conducive to intense and extensive disturbances like the large forest fires that have become common in the western U.S. (Hessburg and Agee 2003). Efforts to desynchronize populations that have become strongly synchronous should compliment basic efforts to maintain large and productive population assemblages. These efforts could entail promoting the existence of a broad distribution and diversity of habitats that support a wide array of life-history forms and ensuring that some habitats are sufficiently spatially disjunct so that risks from catastrophic stochastic events are minimized. Of course, these considerations may be moot for many depressed upriver anadromous stocks unless accompanied by continued efforts to address out-of-basin mortality factors.

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Productive capacity of an artificial stream in the Canadian Arctic: assessing the effectiveness of fish habitat compensation

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Abstract: Few fish habitat compensation projects are assessed with respect to the principle of "no net loss" of productive capacity. Using reference streams as standards against which gains and losses of functions (e.g., production of fish) could be quantified, we examined the effectiveness of a 3.4-km artificial stream in the Northwest Territories, Canada. The artificial stream restored watershed connectivity, allowing fish migration and provided spawning and nursery habitat, particularly for Arctic grayling (*Thymallus arcticus*). However, the average mass of young-of-the-year (YOY) grayling at the end of summer was lower (57%) in the artificial stream than in natural streams. This difference in growth, in concert with estimates of grayling density, meant that the standing crop produced in the artificial stream averaged 37% of that found in natural streams. A bioenergetics model indicated that cooler water temperatures in the artificial stream had limited influence on growth. Instead, low amounts of autochthonous and allochthonous organic matter and poor physical habitat in the artificial stream appeared to limit the productivity of benthic invertebrates and fish. Our explicit analysis of productive capacity will allow future compensation measures to focus on deficiencies in the artificial stream and on the improvement of its productive capacity as fish habitat.

Résumé : Peu de projets de compensation d'habitat de poissons sont évalués en tenant compte du principe qu'il doit n'y avoir "aucune perte nette" de capacité de production. En utilisant des cours d'eau témoins comme points de référence pour quantifier les gains et les pertes fonctionnelles (e.g., la production de poissons), nous avons évalué l'efficacité d'un cours d'eau artificiel de 3,4 km dans les Territoires du Nord-Ouest, Canada. Le cours d'eau artificiel a rétabli la connectivité du bassin hydrographique, permis la migration des poissons et fourni des habitats de fraye et de développement des alevins, en particulier pour l'ombre arctique (*Thymallus arcticus*). Cependant, la masse moyenne de petits ombres de l'année (YOY) à la fin de l'été est plus faible (57 %) dans le cours d'eau artificiel que dans les cours d'eau naturels. Ces différences de croissance, combinées aux estimations de densité, font que la biomasse produite dans le cours d'eau artificiel représente en moyenne 37 % de celle qui existe dans les cours d'eau naturels. Un modèle bioénergétique démontre que les eaux plus fraîches du cours d'eau artificiel n'ont qu'une influence mineure sur la croissance. En revanche, les faibles quantités de matière organique autochtone et allochtone et l'habitat physique inadéquat du cours d'eau artificiel semblent limiter la productivité des invertébrés benthiques et des poissons. Notre analyse explicite de la capacité de production fait en sorte que les mesures de compensation futures pourront cibler les déficiences du cours d'eau artificiel et chercher à améliorer sa capacité de production comme habitat pour le poisson.

[Traduit par la Rédaction]

Introduction

Habitat loss and degradation caused by extraction of natural resources, industrial processing, agriculture, and urbanization threaten the sustainability of fisheries resources. In Canada, the principal legislation for the conservation and management of fisheries and fish habitat is the Fisheries Act. Under this Act, management strategies focus on preventing the harmful alteration, disruption, or destruction (HADD) of habitats that sustain fish productivity. To guide implementation of the Act, the Department of Fisheries and Oceans (DFO) developed a "Policy for the Management of Fish Habitat" (hereafter, the Policy (DFO 1986)). The guiding principle of the Policy is to ensure "no net loss of productive capacity of fish habitats" (NNL; Minns et al. 1996). Productive capacity is defined in the Policy as "the maximum natural capability of habitats to produce healthy fish … or to support or produce aquatic organisms upon

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which fish depend" (DFO 1986, p. 28). When developments that will alter fish habitat are proposed and compensation programs are required, HADD and NNL assume the ability to quantify effects on fish production. This, in turn, presumes that the habitat needs of species are understood, that the relationship between habitat and fish production is known or can be assessed, and that there is an undisturbed natural area or time before disturbance that can serve as a reference and provide a measure of the effectiveness of restorative or enhancement measures (Minns 1997). Frequently, however, one or more of these presumptions are not met. For a variety of reasons, most assessments of habitat compensation must rely on rather indirect measures of program effectiveness (Minns 1997).

Despite the overwhelming importance of NNL to fisheries management in Canada, few studies have evaluated the effectiveness of mitigation measures within this framework. Minns et al. (1996) challenged the scientific rigor of habitat compensation programs and suggested that many are rushed within uncharted ecological territory. Rapid compensation action is often seen as more important than carefully examining alternative avenues of compensation and their eventual effectiveness. Ecological restoration is an emerging science and successful restoration is a serious test of our often limited, ecological understanding; as such, efforts will be fraught with mistakes (Bradshaw 1996). A more rigorous approach to compensation is needed, grounded in the principles of the scientific method, including the use of appropriate reference sites. Peer-reviewed examinations of restoration efforts, both successes and failures, need to be published (Bradshaw 1996; Minns et al. 1996), for only then we can begin to learn from our collective experiences.

In 1991, diamonds were discovered in the remote region of the Northwest Territories known as the Barrenlands. In preparation for mineral extraction, two lakes and their tributary streams within a larger chain of lakes were drained. As part of the habitat compensation agreement, a 3.4-km artificial stream was blasted out of Shield rock. Since 1997, water has been diverted around the two lakes, now open-pit mines, through the artificial stream. The objective of the compensation was to restore watershed connectivity for fish migration and provide spawning and nursery habitats, primarily for Arctic grayling (*Thymallus arcticus*), and thus offset the losses in stream habitat from development.

We based our assessment of this compensation on a hierarchical framework of the specific functions needed by the artificial stream to achieve NNL of productive capacity. Because we lacked an ecological description of the streams lost during development, or even of Barrenland streams in general, the use of natural, undisturbed streams was all the more important for establishing reference conditions and quantifying gains and losses in productive capacity of fish habitat. The relative simplicity of the fish assemblages and the availability of many pristine streams in the region to serve as reference sites provided an unparalleled opportunity to examine the effectiveness of the artificial stream in providing productive fish habitat, as per DFO's guiding principle of NNL. As part of this examination, the main objectives of our study were to (*i*) assess the production of young-of-the-year (YOY) grayling in the artificial stream, relative to natural (reference) streams, in terms of density, growth, and condition, and (*ii*) examine factors that might explain differences in growth between the natural and artificial streams, including water temperature, invertebrate food availability, and physical habitat. We assessed the relative effect of temperature on growth and explored potential effects of food using a bioenergetics model calibrated to field data on YOY Arctic grayling.

Study system

The 4000-km^2 study area is centred around 64°45′N and 110°30′W (see Fig. 1), about 100 km north of the tree line within the southern arctic ecozone. The mean annual temperature is approximately –12 °C, with a summer maximum of 27 °C and a winter minimum of –54 °C (Environment Canada 1991). The climate is semi-arid with 200–300 mm of precipitation annually, 50% of which falls as snow. The region is underlain by granite, gneiss, and schist that form broad, sloping uplands, plateaus, and lowlands. The permafrost layer is continuous. Eskers, kames, and boulder-strewn till plains cover the land. Thin soils in upland areas support dwarf heath and scattered low shrub tundra, whereas lowland and depressional areas near lakes and streams are characterized by sedge tussock and low-tall shrub tundra.

The combination of relatively low topographical relief (~50 m) and extensive glacial activity has molded a landscape covered by about 21% water in the form of numerous chains of lakes and connecting streams. After spring runoff, evaporation from lakes gradually lowers lake levels and stream flows diminish, with many small streams eventually becoming dry. Flows can increase (or resume) in late summer and fall but are frozen solid during the long arctic winter. At ~450 m above sea level (asl), the streams of this area are the headwaters of the Coppermine, Back, and Burnside rivers, which flow north to the Arctic Ocean.

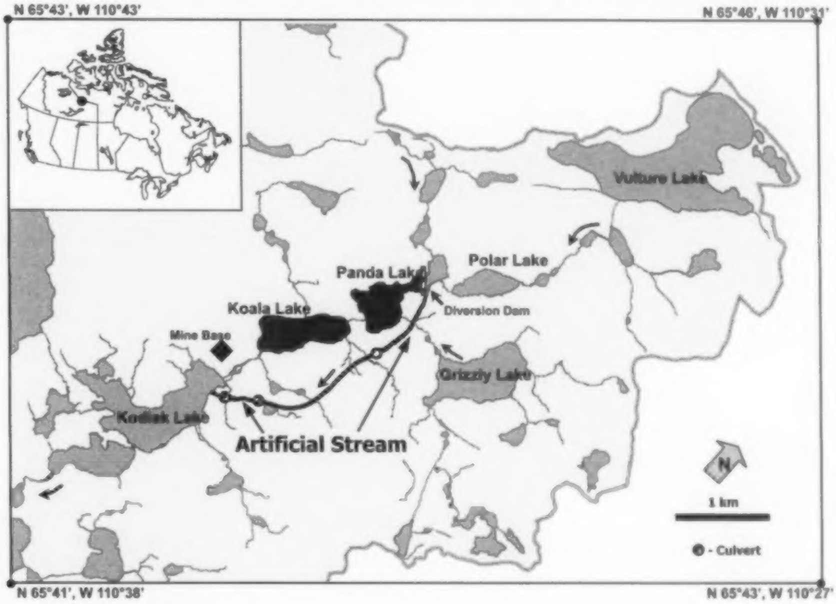
Arctic grayling is well represented in the fish communities, which also include slimy sculpin (*Cottus cognatus*), burbot (*Lota lota*), round whitefish (*Prosopium cylindraceum*), lake trout (*Salvelinus namaycush*), longnose sucker (*Catastomus catastomus*), ninespine stickleback (*Pungitius pungitius*), lake chub (*Couesius plumbeus*), and northern pike (*Exos lucius*). Most streams support at least one species but commonly contain only three species: Arctic grayling, burbot, and slimy sculpin (Jones et al. 2003*a*). Streams are used mainly for spawning and subsequently as nursery habitat for YOY grayling, whereas the numerous lakes in the region are used by all ages and species of fish for overwintering. Fish are known to migrate among lakes and streams during the open-water season (N.E. Jones, unpublished data).

Methods

General sampling design

Data were collected during four summers, 1998 to 2001. Twenty natural streams, distributed throughout the study area and ranging in abiotic and biotic conditions, were surveyed for basic physical characteristics, fish community composition and abundance, and the size of YOY grayling

Fig. 1. Map showing the location of the artificial stream in relation to lakes in the watershed. Koala Lake and the dark portion of Panda Lake were drained and developed as open-pit mines. Water flow, indicated by the arrows, moves from Vulture Lake to Polar Lake through the artificial stream and into Kodiak Lake. Insert: location of study area in the Northwest Territories, Canada.



just before out-migration (see Jones et al. 2003*a*). Reference streams were selected based on the presence of visible water in the stream channel during aerial surveys in late July. A subset of nine natural streams, more centrally located around the artificial stream, were also sampled for benthic invertebrates, water chemistry, woody debris volumes, substrate coarse particulate organic matter (CPOM), and epilithon; two of these streams, Polar–Vulture and Pigeon, were subjected to more intensive fisheries and invertebrate drift investigations. Given their remote arctic location, reference streams were assumed to represent the range of natural structure and function (e.g., production of YOY grayling) for streams in this region. As such, we used reference streams to establish standards against which differences of the artificial stream could be compared. The artificial stream was sampled for all of the above parameters.

Basic stream surveys (stream physical characteristics and fish)

Stream geomorphology, including stream length, slope, bankfull width and depth, and substrate composition, were determined from ground surveys, aerial photographs, and topographic maps. Substrate composition and aquatic vegetation cover were quantified along several transects perpendicular to stream flow, with substrates classified as clay and silt (<0.0625 mm), sand (0.0625–2 mm), small gravel (2–32 mm), large gravel (32–64 mm), cobble (64–256 mm), and boulder (>256 mm). Mesohabitat composition (cascade, riffle, run, flat, pool, wetland, boulder garden, and culvert; Ontario Ministry of Natural Resources (OMNR) 1987) was also quantified as percent length of stream.

Arctic grayling fry were first observed 21 to 24 days after spawning (early July). Swim-up dates, determined as the date on which larval grayling were visible along stream margins and captured in larval drift nets, were similar among streams. At this time, young were 11–13 mm in length and 0.01 g in mass (Jones et al. 2003*a*). During the arctic fall, approximately late August to early September, fish, including YOY grayling, migrate out of streams to overwinter in lakes before streams freeze solid. Hence, by late August, about 50 days after swim-up, YOY grayling mean mass represents a significant percentage of first-year growth.

Fish community composition and the end-of-season size of YOY grayling were determined by electrofishing in late summer (about 23 August), shortly before the out-migration, in one, two, ten, and three natural streams in 1998, 1999, 2000, and 2001, respectively. Captured fish were identified, enumerated, weighed (±0.01 g), and measured (fork length ± 1 mm).

Benthic stream surveys (limnology, woody debris, epilithon, CPOM, and benthic invertebrates)

Three replicate water samples were collected from each stream in late July. Samples were stored in a cold, light-free environment until analysis. In the laboratory, total nitrogen was determined using the persulfate digestion method on a Technicon AutoAnalyzer (Pulse Instrumentation (1992) Ltd., 433 Birch Cres., Saskatoon, SK S7N 2K2). Total phosphorus ($\pm 1\ \mu g \cdot L^{-1}$) was determined spectroscopically using persulfate-oxidized samples by molybdate blue absorption.

Woody debris volumes were determined by counting all woody debris longer than 10 cm along 40- to 150-m lengths of stream channel. We measured the length of each piece and determined the mean diameter by averaging the diameters of each end and converted these dimensions to volume estimates. The surface area of the sampled section was determined by multiplying the transect length by the mean stream width measured at four locations along the stream. Volumes were then standardized to $cm^3 \cdot 100\ m^{-2}$.

Numbers of shrub stems located within 1 m of the stream bank were counted along transects 40–150 m along each stream bank and converted to mean densities (individuals (ind.)$\cdot m^{-2}$). We also used transects to quantify the amount of grass and shrubs along stream banks as a percentage of the ground covered and similarly determined coverage of the streambed by aquatic macrophytes and bryophytes.

Five replicate samples of substrate CPOM, epilithon, and benthic invertebrates were collected in late July from the same locations in both riffles (mean depth, 0.24 m; mean velocity, 0.25 $m \cdot s^{-1}$) and pools (mean depth, 0.34 m; mean velocity, 0.08 $m \cdot s^{-1}$). CPOM samples were collected by inserting a plastic jar, 90 mm deep × 80 mm diameter, vertically into the substratum. Within 48 h, we washed the refrigerated samples, removing inorganic material and invertebrate cases and exuviae, and sieved them through 1-mm mesh. Filtered organics on the screen were then dried to constant mass at 40 °C (±0.1 mg). Periphyton samples were scraped from the upper surfaces (4.9 or 9.6 cm^2) of randomly selected stones. Invertebrates visible without the aid of magnification were removed from scrapings. Samples were stored frozen in the dark for 2–4 weeks before being dried at 40 °C, weighed, ashed at 550 °C, and reweighed for ash-free dry mass determination (±0.1 mg). Benthic invertebrate samples were collected using a 0.093-m^2 Surber sampler, fitted with 250-μm mesh. All samples were preserved with 70% ethanol in the field. Invertebrates were identified to genus or species, with the exception of Nematoda, Turbellaria, and terrestrial invertebrates, which were typically identified to family or order. Following enumeration, samples were dried to constant mass at 40 °C and weighed (±0.1 mg).

Intensive stream sampling (temperature, drift, fish growth, biomass, and density)

HOBO temperature loggers synchronously recorded stream water temperature (±0.1 °C) every 4 h from freshet to late August in the artificial (five locations) and Polar–Vulture and Pigeon (two locations each) streams.

The amount and composition of cover available for YOY grayling were visually estimated using transects perpendicular to the axis of the stream. The streams were divided into 10-m sections, and a transect was placed randomly within each section. Cover types, which provide one or a combination of velocity refuge, visual isolation, or overhead cover (sensu Fausch 1993), included depth, turbulence, rock, undercut, aquatic vegetation, and terrestrial vegetation.

Drift was sampled simultaneously at two locations within each stream with Field-Dodgson tri-net samplers, fitted with 250-μm nets. On each sampling date (15 and 30 July, 15 and 29 August), drift was collected at dawn, noon, and dusk. Samples were collected from relatively shallow water (mean depth and velocity, 0.16 m and 0.24 $m \cdot s^{-1}$, respectively) in close proximity to fish collection areas to reflect organisms available to grayling. Nets were wetted for 30–45 min, depending on flow rates, to filter 3–6 m^3 of water. To determine sample volumes, we measured water velocities at the mouth of each sampler using a Swoffer Model 2100 current velocity meter (Swoffer Instruments, Inc., 1048 Industry Drive, Seattle, WA 98188). Drift samples were preserved in 70% ethanol and later identified and counted. After enumeration, samples were dried to constant mass at 40 °C and weighed (±0.1 mg).

Invertebrates in the drift were classified as either large (e.g., insects) or small (e.g., microcrustaceans) based on body mass. Head capsule width (±0.01 mm), an indicator of invertebrate body mass, was measured on Chironomidae and Simuliidae larvae from a random subset of drift samples from each date in year 2000 using a dissecting scope equipped with an ocular micrometer.

In the artificial and Polar–Vulture streams, we estimated total fish density ($fish \cdot m^{-3}$) and biomass ($g \cdot m^{-3}$) in late July 1998–2000 using the three-pass removal method, with habitat stratified as pools and riffles. Captured fish were identified, enumerated, weighed (±0.01 g), and measured (fork length ± 1 mm). Volumes electrofished were determined for each section shortly after being surveyed. Computations for population estimates were made separately for Arctic grayling (juvenile and YOY), slimy sculpin, and burbot. For each section of stream, we estimated total fish biomass per species by multiplying the mean individual mass by the number of fish estimated for that section. Upwards of 75% of the estimated total fish abundance were typically captured in each fished section of stream.

Aside from the estimates of first-year growth of YOY Arctic grayling before out-migration (see Basic stream surveys), the mean mass of YOY grayling was also determined several times from swim-up to shortly before out-migration in the artificial, Polar–Vulture, Pigeon, and Polar–Panda streams.

Finally, the diet of YOY grayling from the artificial stream was determined using methods of Jones et al. (2003*b*); briefly, 19 invertebrate taxa were identified in the stomachs and subsequently classified as either large or small based on body size. To examine prey size selection, we measured head capsule widths on the two most commonly consumed invertebrate taxa, Chironomidae and Simuliidae, from random subsets of stomach samples from each sampling period in 2000. We used a dissecting scope equipped with an ocular micrometer for measurements (±0.01 mm). We have included some reference stream data from Jones et al. (2003*b*) for a comparison with the food habits of YOY grayling from the artificial stream.

Bioenergetic model and simulations

We used bioenergetics modelling to assess the relative effects of different water temperatures in artificial and natural streams on observed growth of YOY Arctic grayling (see Ries and Perry 1995; Railsback and Rose 1999). We used the Wisconsin model (Fish bioenergetics 3.0; Hanson et al. 1997), configured for age-0 Arctic grayling (Table 1). Model inputs were average daily temperatures from swim-up to 23 August and the respective mean mass of the YOY grayling on these sampling dates.

Table 1. Physiological parameters used in the bioenergetics model for young-of-the-year Arctic grayling.

Parameter	Value	Reference
Waste losses (eq. 1)[a,b]		
FA — egestion	0.15	Hanson et al. (1997)
UA — excretion	0.1	Hanson et al. (1997)
Respiration (eq. 2)[a,c]		
RA — grams of oxygen ($g \cdot g^{-1} \cdot day^{-1}$) consumed by a 1-g fish at RTO	0.0156	Harrison (1995)
RB — slope of allometric mass function	–0.287	Harrison (1995)
RQ — (°C^{-1}) approximates Q_{10}	2.1	Harrison (1995)
RTO — (°C) optimal temperature for respiration	18	Harrison (1995)
RTM — (°C) maximum lethal temperature	26.4	Harrison (1995)
SDA — specific dynamic action	0.172	Hanson et al. (1997)
Activity	1.3	Hanson et al. (1997)
Consumption (eq. 3)[a,c]		
CA — intercept of the mass dependence	0.628	Rand et al. (1993)
CB — coefficient of the mass dependence	–0.3	Rand et al. (1993)
CQ — (°C) lower water temperature at which the temperature dependence is a small fraction (CK1) of the maximum consumption rate	5	Rand et al. (1993)
CK1 — small fraction of the maximum consumption rate	0.33	Rand et al. (1993)
CTO — (°C) temperature corresponding to 0.98 of the maximum consumption rate	20	Rand et al. (1993)
CTM — (°C) temperature (≥ CTO) at which dependence is still 0.98 of the maximum consumption rate	20	Rand et al. (1993)
CTL — (°C) upper water temperature at which temperature dependence is a small fraction (CK4) of the maximum consumption rate	24	Rand et al. (1993)
CK4 — small fraction of the maximum consumption rate	0.2	Rand et al. (1993)

[a] Hanson et al. (1997).
[b] Kitchell et al. (1977).
[c] Thornton and Lessem (1978).

In our bioenergetic simulations, we first adjusted food consumption (P value) to meet the observed final mass observed in each stream using their respective temperature regimes. We then determined what the final mass for a YOY grayling would be if we substituted the temperature regime in the artificial stream for that observed in the natural stream. Secondly, we asked what the final mass would be if we substituted the P value observed in the artificial stream for that observed in the natural stream? We estimated the effect of temperature on the growth (Growth_T), as

$$\mathrm{Growth}_T = \left[\frac{\left|\mathrm{OBS}_{\mathrm{ART}} - \mathrm{PRE}_{P_{\mathrm{art}} \& T_{\mathrm{nat}}}\right|}{\mathrm{OBS}_{\mathrm{NAT}} - \mathrm{OBS}_{\mathrm{ART}}}\right] \times 100\%$$

where $\mathrm{OBS}_{\mathrm{NAT}}$ and $\mathrm{OBS}_{\mathrm{ART}}$ are the observed mass of YOY grayling on 23 August in the natural and artificial stream, respectively, and $\mathrm{PRE}_{P_{\mathrm{art}} \& T_{\mathrm{nat}}}$ is the predicted mass of grayling based on the P value from the artificial stream (P_{art}) and the temperature regime from the natural stream (T_{nat}). We estimated the effect of food availability on the growth (Growth_F) as

$$\mathrm{Growth}_F = \left[\frac{\left|\mathrm{OBS}_{\mathrm{ART}} - \mathrm{PRE}_{P_{\mathrm{nat}} \& T_{\mathrm{art}}}\right|}{\mathrm{OBS}_{\mathrm{NAT}} - \mathrm{OBS}_{\mathrm{ART}}}\right] \times 100\%$$

where $\mathrm{OBS}_{\mathrm{NAT}}$ and $\mathrm{OBS}_{\mathrm{ART}}$ are the observed mass of YOY grayling on 23 August in the natural and artificial streams, respectively, and $\mathrm{PRE}_{P_{\mathrm{nat}} \& T_{\mathrm{art}}}$ is the estimated mass of grayling based on the P value from the natural stream (P_{nat}) and the temperature regime from the artificial stream (T_{art}). Our ability to determine the influence of temperature is imperfect in that there is an indirect effect of temperature on $C_{\max}$, the maximum specific feeding rate. However, for the purposes of this study, this indirect effect of temperature is likely small, particularly over the relatively short simulation times used in this study. We also conducted sensitivity analyses for the P value and activity multiplier by changing these inputs by 25, 50, and 100%.

Statistical analyses

We employed one-sample hypotheses testing (OSH; Sokal and Rohlf 1995), using data from general and benthic stream surveys (e.g., substrate, cover, water chemistry, epilithon, CPOM, benthic invertebrates), for comparisons between the artificial and natural streams. Our interest was in comparing the average value of a measured variable from the artificial stream with the distribution of values among natural streams. When the number of natural streams sampled was limited, we used general linear modelling (GLM) followed by Tukey's multiple comparison tests for comparisons between the artificial and reference streams (e.g., fish, invertebrate drift, head capsule size). Analysis of covariance (ANCOVA) was used to determine if YOY were of different condition (mass-at-length) among streams and years; mass–length data were square root transformed. We used the Kolmogorov–Smirnov test to examine data for normality and the Levene median test for homogeneity of variances. For all statistical tests, we used $\alpha = 0.05$ as a critical level of signifi-

Table 2. Mean percentage total cover (± standard error) and its distribution among cover types available to young-of-the-year Arctic grayling in the artificial stream and two natural streams, Polar–Vulture and Pigeon.

		Cover types					
Stream	Total cover	Rock	Depth	Turbulence	Aquatic vegetation	Undercut	Terrestrial vegetation
Artificial	22	39	26	34	0	1	0
Natural	42 (0.3)	24 (3.5)	22 (7.7)	18 (0.0)	22 (3.2)	8 (1.4)	6 (0.3)
Significance	0.009	0.140	0.721	0.001	NA	0.021	NA

Note: Significance (*P* value) indicates differences between the artificial and natural streams (one-sample hypothesis testing). Aquatic and terrestrial vegetation were very scarce in the artificial stream. NA, not applicable.

Table 3. Temperature regime characteristics of the artificial (ART) and natural streams, Polar–Vulture (PV) and Pigeon (PG), from swim-up of young-of-the-year Arctic grayling to 31 August 1998–2001.

	19 June 1998 (n = 74)		5 July 1999 (n = 57)		30 June 2000 (n = 62)			6 July 2001 (n = 53)	
	ART	PV	ART	PV	ART	PV	PG	ART	PV
Mean temperature (°C)	13.3 (2.3)	14.0 (2.3)	11.0 (2.0)	12.0 (2.1)	13.5 (3.8)	14.6 (3.9)	14.1 (4.1)	13.3 (3.5)	14.2 (3.5)
Total degree-days	983	1038	629	685	834	903	877	704	751
Mean difference (°C)		0.7 (0.4)		1.0 (0.3)		1.1 (0.5)	0.7 (0.7)		0.9 (0.0)
Sum of differences (degree-days)		54.9		56.7		69.4	43.0		47.7

Note: Mean temperature is the overall seasonal average of mean daily temperatures, which are the average of six measurements per day. Mean difference is the difference in mean daily temperatures between natural stream(s) and the artificial stream, averaged over the season. The mean daily temperature in the artificial stream was significantly lower (paired *t* tests, $P < 0.05$) in all comparisons with natural streams. Standard errors are in parentheses. *n*, number of days from swim-up date to 31 August.

cance (after performing the Bonferroni adjustment, when required to reduce the experimentwise error rate).

Results

Physicochemical

Large-scale differences in habitat between the artificial and reference streams include mesohabitat composition and the number of side channels. Although natural streams that drain areas of fine sediment tend to have single, well-defined channels, most natural streams in the Barrenlands are multichannelled, with some streams having more than six side channels. In contrast, the artificial stream was constrained by steep (10–90°) and high (2–10 m) banks, with a single channel throughout its entire length. Natural streams typically contain a diversity of mesohabitat types. Despite its length (3.4 km), however, the artificial stream has a limited number of habitat types, with wetland and boulder garden absent. In addition, the proportions of the habitat types differ from those found in reference streams. For example, natural streams had more riffles (33 vs. 4%) and pools (11 vs. 1%), whereas the artificial stream had more cascades (7 vs. 1%) and flats (55 vs. 18%) (OSH; df = 19, $P < 0.05$). Cover for YOY grayling in reference streams was nearly double that found in the artificial stream (Table 2). In addition, the cover types available to grayling were more diverse in the natural streams than in the artificial stream, where vegetation (aquatic and terrestrial) was almost entirely absent (Table 2).

Substrate sizes in the artificial stream were significantly smaller than those found in the reference streams. Fine substrates (silt, clay, and sand) dominated 44% of the substrate composition in the artificial stream, whereas in the natural streams, fines composed only 14%; the proportion of sand was significantly greater in the artificial stream (OSH; df = 19, $P < 0.05$). Moreover, boulders composed only 16% of the substrate in the artificial stream but 56% in natural streams (OSH; df = 19, $P < 0.05$).

Water chemistry in the artificial stream was similar to that found in natural streams. Total phosphorus in the artificial stream was not significantly different from that measured in natural stream systems (9.85 and 6.92 $\mu g \cdot L^{-1}$ ± 0.72 standard error (SE), respectively; OSH; df = 5, $P < 0.05$). However, total nitrogen was higher in the artificial stream than in the natural stream systems (321.56 and 167.20 $\mu g \cdot L^{-1}$ ± 26.7 SE, respectively; OSH; df = 5, $P < 0.05$). At times, particularly during high flow events (spring and fall), turbidity and suspended solids levels would briefly but dramatically increase in the artificial stream (N.E. Jones, personal observation).

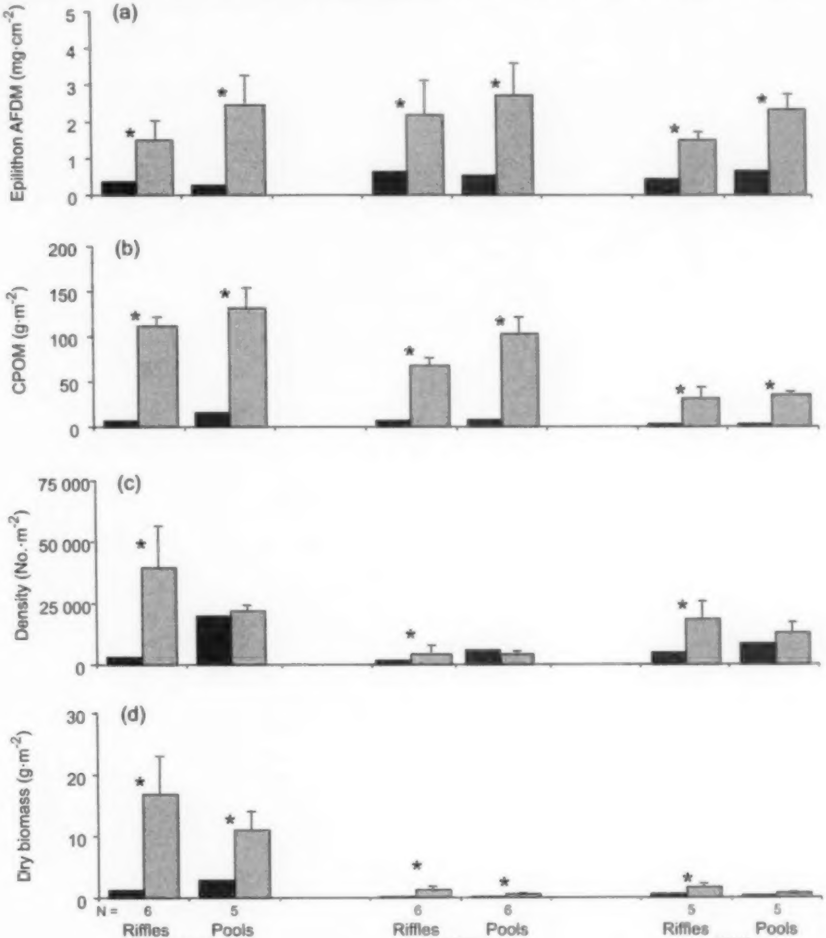
Natural streams accumulated a mean of 851 degree-days from swim-up of YOY Arctic grayling to 31 August (Table 3). Daily water temperatures in the artificial stream averaged 0.9 °C colder than in the natural streams during the growth period (Table 3). This seemingly small difference accumulated to an average deficit of 56 degree-days from swim-up to out-migration in late August.

Biological

Vegetation and organic matter

A major difference between the artificial and reference streams is in the amount of living and dead plant material in the stream channels and adjacent riparian areas. The riparian zones of natural Barrenland streams are generally well vegetated. In well-drained riparian zones, dwarf heath and scattered low shrub tundra dominate, whereas sedge tussock is common in poorly drained areas. In contrast, the riparian

Fig. 2. Mean (± standard error) amounts of (*a*) epilithon and (*b*) substrate coarse particulate organic matter (CPOM) and benthic invertebrate (*c*) density and (*d*) biomass in riffle and pool habitats from the artificial (solid bars) and natural streams (shaded bars), 1998–2000. Asterisks indicate significant differences (*t* test, $P < 0.05$) between stream types. AFDM, ash-free dry mass.

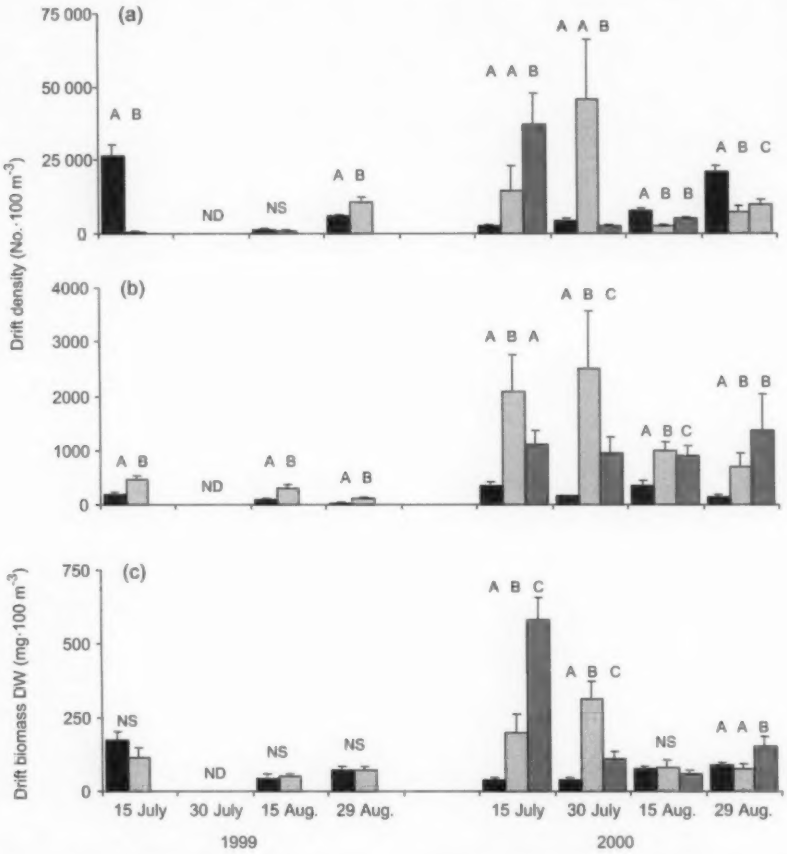


zone of the artificial stream is dominated by a thick layer of blast rock, although willow plugs have been planted to stabilize banks in a few areas. Grasses covered 44% (± 5% SE) of the ground in natural riparian zones, but only 4% in the artificial (OSH; df = 8, $P < 0.05$). Similarly, cover by shrubs averaged 58% (± 5% SE) in natural riparian zones but only 1% in the artificial stream (OSH; df = 8, $P < 0.05$). The average density of shrub stems within 1 m of the stream was $0.86{\cdot}m^{-2}$ (± 0.12 SE) and $0.06{\cdot}m^{-2}$ in the reference and artificial streams, respectively (OSH; df = 8, $P < 0.05$).

Aquatic plants, consisting of macrophytes, algae, and bryophytes, were generally abundant in natural streams but were rare in the artificial stream, and those that existed in the latter were mostly planted. Epilithon abundance, particularly *Zygnema* spp., was significantly greater in the natural streams compared with the artificial stream (OSH; $P < 0.05$; Fig. 2*a*). Depositional areas of fine substrate organic matter in natural streams also supported an abundance of aquatic macrophytes (e.g., bur-reed (*Sparganium hyperboreum*) and mare's-tail (*Hippuris vulgaris*)), covering 17% (± 5% SE) of the streambed by mid-July. Macrophytes in the artificial stream consisted of planted Arctic pendant grass, *Arctophila fulva*, which thinly covered only 1% of the streambed. Bryophytes were common in some natural streams, covering 10% (± 3% SE) of the streambed, but were absent from the artificial stream.

Stemming from a lack of riparian vegetation, the artificial stream contained about one-tenth of the coarse particulate organic matter (CPOM) found in the natural streams (OSH; $P < 0.05$; Fig. 2*b*). In the natural streams, many sections of riffle pass through thick growths of dwarf birch and willow, which contribute relatively small pieces of woody debris (mean length and diameter, 370 and 5 mm, respectively) to the channel. Woody debris volume in the artificial stream, $215\ cm^3{\cdot}100\ m^{-2}$ of streambed, was about fourfold lower than that in the natural streams, $917 \pm 350\ cm^3{\cdot}100\ m^{-2}$

Fig. 3. Mean (± standard error) densities in the drift of (*a*) small (e.g., microcrustaceans) and (*b*) large (e.g., insects) invertebrates and (*c*) total drift biomass (dry mass (DM)) in the artificial (solid bars) and natural streams, Polar–Vulture (light shaded bars) and Pigeon (darker shaded bars), during four sampling periods in 1999–2000. Letters indicate significant differences among streams (general linear modelling and multiple comparisons, $P < 0.05$) for each time period; $N = 18$ per stream and time period; NS, not significant; ND, no data.



(mean ± SE). Essentially, all woody debris in the artificial stream were willow plugs added as remediation during 1998–2000.

Invertebrates

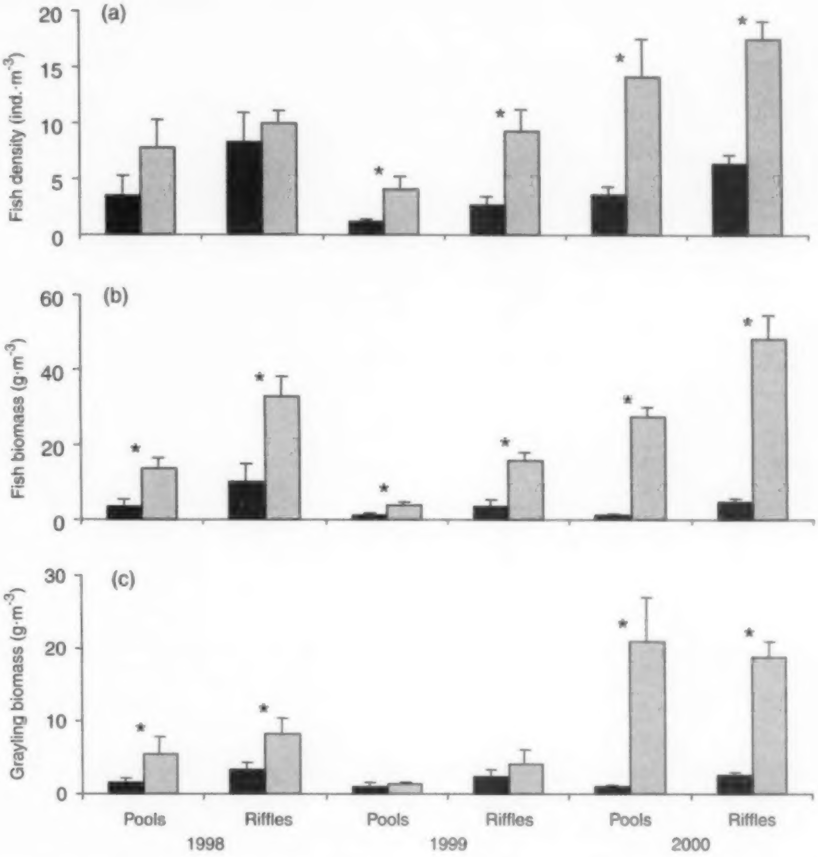
Although there was considerable variation among streams and years, higher numbers of benthic invertebrates were generally contained in the natural streams than in the artificial stream, especially in riffles (OSH; $P < 0.05$; Fig. 2*c*). Differences were even greater for benthic invertebrate biomass estimates (OSH; $P < 0.05$; Fig. 2*d*), suggesting that the benthic invertebrates in the natural streams were larger. Dipterans were well represented in all streams, contributing about 45% of all individuals and 62% by mass, 19% of which were chironomids.

The numbers of small invertebrates (e.g., microcrustaceans, including cladocerans, copepods, and ostracods) in the drift did not differ between the artificial and natural streams (GLM; $n = 18$ per date and stream, $P > 0.05$; Fig. 3*a*). However, there were significantly fewer large organisms (e.g., insect larvae, including chironomids, simuliids, and ephemeropterans) in the drift of the artificial stream on all sampling dates compared with natural streams (GLM; Fig. 3*b*). Mean drift biomass in the artificial and natural streams was similar in 1999. In 2000, however, drift biomass in natural streams was typically higher (GLM; Fig. 3*c*). As suggested above, the head capsule widths of drifting larval Chironomidae were larger in the natural streams (Polar–Vulture and Pigeon) than in the artificial stream (GLM; df = 223, $P < 0.05$); however, larval Simuliidae size was similar among streams (GLM; df = 252, $P = 0.06$).

Fish

Spawning surveys and radiotelemetry studies indicated that adult and juvenile Arctic grayling were able to migrate successfully through the artificial stream and its three culverts (N.E. Jones, unpublished data). Other species and age-classes, including slimy sculpin and burbot, were unable to ascend a second culvert, 700 m upstream from Kodiak Lake (Fig. 1). Depending on the year, between 200 and 300 grayling were observed migrating into the artificial stream. Although a quantitative estimate of spawning success was not determined, YOY grayling were produced in relatively

Fig. 4. Mean (± standard error) (*a*) density (ind., individuals) and biomass of (*b*) all fish and (*c*) grayling in pool and riffle habitats in the artificial (solid bars) and Polar–Vulture (shaded bars) streams in 1998–2000. Asterisks indicate significant differences (*t* tests; $P < 0.05$) between streams.



large numbers, particularly in the lower end of the stream where most of spawning occurred (N.E. Jones, unpublished data).

Fish communities: density and biomass

Fish community composition in the artificial stream was similar to that in the intensively fished natural stream, Polar–Vulture. Age-0 grayling dominated both communities, numerically and by biomass. Other species in both streams included slimy sculpin and burbot. Total densities of fish in the artificial stream were similar to (1998) or less than (1999, 2000) densities found in Polar–Vulture (GLM; df = 55, $P < 0.05$; Fig. 4*a*). In contrast, fish biomass was consistently and significantly greater in Polar–Vulture on all dates (GLM; df = 55, $P < 0.05$; Fig. 4*b*). Similarly, grayling biomass was generally greater in Polar–Vulture (GLM; df = 55, $P < 0.05$; Fig. 4*c*).

Growth and production of age-0 grayling

Growth varied considerably among years, related to differences in temperature, discharge, and invertebrate densities (Table 4). The two most intensively studied reference streams, Polar–Vulture and Pigeon, produced the slowest- and fastest-growing YOY grayling, respectively, among natural streams. By 23 August, before out-migration, YOY in natural streams averaged 2.74 g ± 0.44 SE, whereas YOY in the artificial stream were only 1.18 g ± 0.14 SE (Table 5). Differences in growth between the artificial and natural streams became more prominent over the course of a summer (Fig. 5a). Analysis of covariance indicated a significant interaction ($P = 0.003$) between the covariate (length) and the independent factor (stream), indicating that the growth rates differed between the artificial and natural streams (Fig. 5*a*). There appears to be little difference in condition (i.e., mass-at-length) among streams and years (Fig. 5*b*). Hence, YOY from different streams followed similar allometries but not at the same rate. The large difference in growth, combined with estimates of YOY grayling density, meant that standing crop in the artificial stream averaged 37% of that found in Polar–Vulture (Fig. 4*c*).

Diet analyses

The composition of invertebrates in the diets of YOY grayling was stream dependent. Grayling stomachs from the artificial stream and Polar–Vulture contained a very similar composition of invertebrates, roughly 75% chironomids and 10% simuliids, whereas fish from Pigeon contained 33% chironomids and 46% simuliids. The head capsule widths of

Table 4. Annual variation in weather and discharge during June–August and accumulated degree-days from spawning to 23 August in relation to mean (± standard error) epilithon mass and mean (± standard error) benthic invertebrate density for Polar–Vulture, Pikejaw, and Slipper – Lac de Gras streams for 1998–2001.

Characteristics	1998	1999	2000	2001	*P* value and post hoc tests
Abiotic					
Accumulated rainfall (mm)	88	180	118	134	
Mean discharge ($m^3 \cdot s^{-1}$)	0.03	0.14	0.13	0.16	
Accumulated mean monthly air temperature (°C)	37	28	34	31	
Mean daily water temperature (°C)	13	12	14	14	
No. of degree-days from spawning to 23 August	1137	882	1029	934	
Biotic					
Epilithon ($mg \cdot cm^{-2}$)	1.7 (0.7)	2.0 (0.6)	1.9 (0.4)	—	0.94
Benthic density ($individuals \cdot m^{-2}$)	31 480 (7541)	3420 (565)	13 720 (1891)	—	0.023 A B A B
YOY length (mm)	77	57 (0.5)	64 (0.9)	56 (0.47)	<0.01 A B C B
YOY mass (g)	3.80	1.78 (0.05)	2.55 (0.12)	1.78 (0.04)	<0.01 A B C B

Note: Data on young-of-the-year (YOY) mean size (± standard error) are from Polar–Vulture. For 1998, fish mass on 23 August was estimated based on two prior sampling periods (9 and 30 July). General linear modelling and multiple comparisons were used to assess differences in biotic characteristics among years.

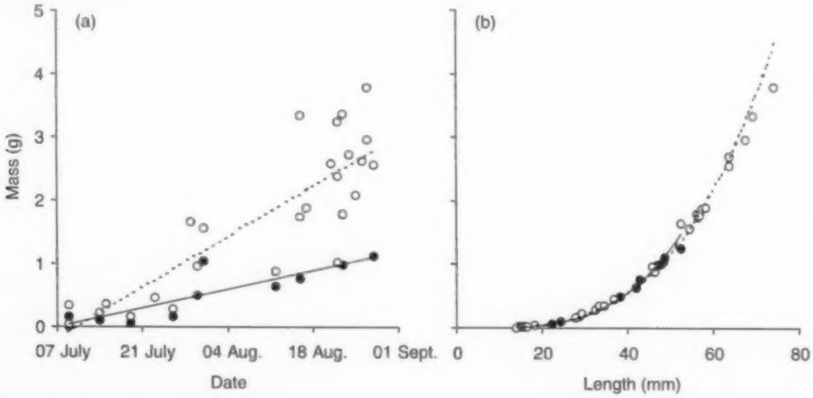
Table 5. Mean mass (g, ± standard error (SE)) and the absolute and relative difference in mass of young-of-the-year Arctic grayling between the artificial and natural streams on 23 August 1998–2001, shortly before out-migration.

Year	1998[a]	1999	2000	2001	Mean	SE
Artificial	1.60	0.99 (0.02)	1.11 (0.09)	1.01 (0.06)	1.18	0.14
Natural	3.80	2.07 (0.11)	2.91 (0.09)	2.12 (0.2)	2.74	0.44
Difference	−2.20	−1.08	−1.80	−1.11	−1.55	0.27
Relative difference (%)	58	48	38	48	57	2.5

Note: Number of natural streams studied per year: 1998, 1; 1999, 2; 2000, 9; 2001, 3.

[a] Fish mass on 23 August 1998 was estimated based on two prior sampling periods (9 and 30 July).

Fig. 5. The mass of young-of-the-year Arctic grayling (*Thymallus arcticus*) in relation to (*a*) date and (*b*) fork length for the artificial (solid line and solid circles) and natural streams (broken line and open circles). All mass and length data points are means of samples collected during the summers of 1998–2001.



Chironomidae (GLM; df = 333, $P < 0.05$) and Simuliidae (GLM; df = 304, $P < 0.05$) in the diets were larger on 50% of sampling dates in the natural streams (Polar–Vulture and Pigeon) versus the artificial stream.

Bioenergetic simulations

Our simulations estimated that 11% of the difference in the mass of YOY grayling between the artificial and natural streams could be attributed to the cooler temperature of the artificial stream, whereas 80% can be attributed to reduced food consumption. The relative importance of temperature varied by year (Table 6). During cooler summers (e.g., 1999), temperature had more of an influence on growth, but during warm summers (e.g., 2000), temperature had little bearing on differences in growth (Table 6).

Our sensitivity analysis of the bioenergetics model indicated that a 50% increase in the *P* value resulted in a fourfold increase in body mass, and a 100% increase resulted in

Table 6. Results of bioenergetics simulations for 1998–2001.

	1998[a]	1999	2000	2001[b]		
Artificial vs. →	PV	PV	PV	PG	PV	Mean
Temperature	13	19	4	2	9	11
Food	81	69	81	93	84	80

Note: Relative influence of temperature and food on young-of-the-year Arctic grayling growth as estimated from the simulations. Natural streams are Polar–Vulture (PV) and Pigeon (PG).

[a] Mass on 23 August was estimated. See Table 5.

[b] Temperatures used in simulations are estimated from those of the artificial stream (artificial stream temperatures plus the mean daily average difference, 0.9 °C).

a 13-fold increase in body mass and thus could contribute to the observed differences in growth between the artificial and natural streams. The bioenergetics model was less sensitive to changes in the activity multiplier. A 50% increase in activity resulted in approximately a twofold reduction in body mass, and a 100% increase resulted in a sevenfold reduction in body mass.

Discussion

Assessing the artificial stream as productive fish habitat

Our assessment of the artificial stream is based on a hierarchical framework of stream functions focused on the production of YOY Arctic grayling: can grayling successfully migrate through the channel, do the grayling spawn in the channel, do the eggs hatch, and do the young grayling grow to a sufficient size? Each function is needed if the artificial stream is to compensate for lost habitat and result in NNL of productive capacity. Reference streams provided standards and therefore enabled us to measure effectiveness.

The artificial stream met or approached our expectations for some of these functions. Although not quantified in this study, we observed that watershed connectivity was at least partially restored and this allowed adult grayling and lake trout to migrate throughout the drainage basin, i.e., the artificial stream restored landscape-scale habitat use (N.E. Jones, unpublished data). Because Barrenlands grayling, with their adfluvial life history, migrate among the chains of lakes and streams in the watershed, its fragmentation would mean the loss of habitat availability at this scale, which could have significant population-level consequences (Kentaro and Shoichiro 2002). As such, restoring watershed connectivity was paramount in the development of the artificial stream. Efforts to maintain a bidirectional fish weir were beset with technical difficulties; however, we estimated that 200–300 adult grayling migrated annually into the artificial stream at ice-out. Within the artificial stream, fish passage was needed so that grayling could move to and select among available spawning areas. Although passage throughout the artificial stream was achieved for adult grayling and lake trout, slimy sculpin and burbot appeared unable to ascend one of the culverts, suggesting that their populations in the watershed have become fragmented.

A quantitative estimate of spawning success was not determined, but we noted qualitatively that YOY grayling were produced in large numbers, particularly in the lower end of the stream where most of the spawning occurred (N.E. Jones, unpublished data). Despite these successes, the growth and production of YOY grayling strongly suggests that the quality of nursery habitat is currently deficient in some manner, e.g., food production, physical habitat, or water temperature, and this deficiency is the focus of our subsequent discussion.

Growth of YOY Arctic grayling

Temperature

Water temperature influences the growth of fish both directly, through physiological processes, and indirectly by affecting rates of energy flow and nutrient dynamics. Water temperature in the artificial stream is, on average, 1 °C colder than that observed in natural streams. The cooler temperatures likely result from less direct sunlight reaching the artificial stream because of steep and high stream banks and because the streambed penetrates deep into permafrost. In contrast, natural Barrenland streams flow through wide shallow valleys and tend to spread laterally. Thus, even with the low angle of incidence of sunlight characteristic of high latitudes, natural streams are almost always well lit throughout the long summer days of the Arctic.

Our bioenergetics simulations nevertheless suggest that summer water temperatures had little influence on the differences in growth. On average, only 11% of the difference in the mass of YOY grayling can be attributed to the cooler temperature of the artificial stream. Other factors, namely food availability and possibly physical habitat, are clearly more important than temperature. Similarly, summer growth of rainbow trout (*Oncorhynchus mykiss*) in the Sierre Nevadas was not directly related to temperature (Railsback and Rose 1999). Although the growth of YOY salmonids in streams can be affected by temperature, particularly when it affects emergence times and thus the length of the growing season (Holtby 1988), emergence in the artificial stream was unaffected.

Nutrients and energy resources

In contrast to the limited effect of temperature, our bioenergetic simulations indicated that differences in food consumption could explain about 80% of the difference in growth of YOY grayling between the artificial and natural streams, suggesting that food availability differed. The well-vegetated banks of natural streams contrast sharply to the waste rock used to line the channel and riparian zone of the artificial stream. Although concentrations of commonly limiting nutrients (phosphorus and nitrogen) in the artificial stream are similar to or greater than those measured in natural streams, the waste rock in the artificial stream supports little algal growth. The artificial stream is also lacking the large amounts of aquatic macrophytes found in natural streams. It seems likely that this paucity of sources of allochthonous and autochthonous organic matter is ultimately a major contributor to the reduced growth and production of YOY grayling in the artificial stream. Moreover, it is likely that the habitat needed by terrestrial and aquatic plants is not currently available and that successional processes are required for their persistence, even if they would be manually introduced. In addition, high flows in the spring and fall result in heavy scour and erosion, further hampering plant colonization and growth (Waters 1995).

In turn, the lack of terrestrial and aquatic plant growth leads to low amounts of particulate organic matter and woody debris. Unlike alluvial streams, where channel migration plays an important role in woody debris recruitment, stream channels in Barrenland streams are generally stable, permafrost-bound, and boulder-dominated colluvial systems, i.e., fluvial process are relatively ineffective at removing material deposited on the valley floor. Natural processes that recruit CPOM and woody debris in natural Barrenland streams include fluvial transport of floodplain organic matter, leaf fall, and Barrenland caribou (*Rangifer tarandus*) that when migrating across the streams trample the riparian shrubs and kick pieces into the stream (Jones et al. 2003*a*). However, the floodplain, and its crossing by caribou, in the artificial stream is extremely limited because of its deeply incised channel design.

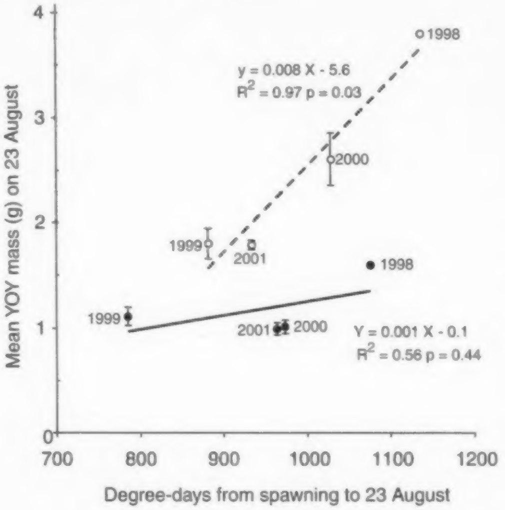
The importance of plants and organic matter as food and substrate for stream invertebrates is well known (Egglishaw 1964; Reice 1980; Flory and Milner 1999). The density and biomass of benthic invertebrates were much reduced in the artificial stream, leading to low drift densities of macroinvertebrates. In addition, the head capsules of chironomids were often smaller in the artificial stream, suggesting food limitation at this trophic level. Successful colonization and growth of invertebrates will also depend on the development of suitable habitat; unassisted, this process will likely require many years before the benthic invertebrate community resembles that in natural streams (Milner et al. 2000). Also, heavy sediment pulses and bed scouring likely damage invertebrate assemblages and hamper invertebrate establishment and growth (Waters 1995; Shaw and Richardson 2001).

Young-of-the-year Arctic grayling in natural Barrenland streams selected aquatic insect larvae, particularly chironomids and simuliids, as primary prey, whereas smaller microcrustacea, nematodes, and mites were strongly avoided (Jones et al. 2003*b*). Further, the sizes of chironomids and simuliids in the stomachs of grayling were frequently larger than those available in the drift, indicating a strong size-based foraging strategy. These forage preferences, and the reduced numbers of large-sized prey available in the drift of the artificial stream, support the hypothesis that the forage base for grayling is limiting their growth in the artificial stream.

Annual variability in temperature and production

Invertebrate drift and benthic invertebrate density and biomass varied considerably among the four study years in relation to air and water temperature, rainfall, and discharge. Correspondingly, YOY grayling were larger in the warm, dry year (1998) when food (i.e., macroinvertebrates) was plentiful. Conversely, epilithon abundance was low, perhaps because of high invertebrate numbers. The opposite pattern was observed in the cool, wet year (1999). These relationships are consistent with those observed recently among discharge, water temperature, and growth of YOY grayling in Alaska (Deegan et al. 1999).

Fig. 6. Mean mass (± standard error) of young-of-the-year (YOY) Arctic grayling (*Thymallus arcticus*) on 23 August in relation to the number of degree-days (water temperatures above 0 °C) accumulated by the artificial (solid line and solid circles) and Polar–Vulture (broken line and open circles) streams between the date of spawning by grayling to 23 August. Masses on 23 August 1998 were estimated for both streams from large samples collected on 9 and 30 July 1998. Also indicated are least-squares regression lines and equations.



The importance of climate in relation to stream productivity and fish growth is evident from the strong relationship between growing degree-days and end-of-season fish mass in Polar–Vulture stream (Fig. 6). The strength of the relationship suggests that fish growth is affected more by climatic factors controlling annual productivity than by the direct effects of temperature on fish physiology. In the artificial stream, however, the relationship between grayling growth and climate is greatly muted. We suggest that food limitation, based ultimately on a paucity of organic matter and suitable habitat for invertebrates, masks the influence of climate in the artificial stream; i.e., the system is unable to respond to the more favourable conditions of a warm, dry year by producing larger YOY fish.

Physical habitat

Relative to the reference streams, habitat complexity at small and large scales was considerably reduced in the artificial stream. The artificial stream had only one fairly straight channel and was deficient in or lacked several mesohabitat types, comparable with many perturbed rivers that have lost channel structure, complex banks, and important snag habitat (Sedell and Froggatt 1984; Benke et al. 1985; Mitro and Zale 2002). At small scales, the artificial stream lacked large substrates, woody debris, and aquatic and terrestrial vegetation, which can create hydraulically complex flows, including flow refuges that provide habitat for YOY grayling, invertebrates, and other aquatic life. Large substrates also provide a stable surface area and interstitial space for invertebrates relative to small substrates; as such, they frequently harbour greater numbers and biomass and a diversity of benthic invertebrates (e.g., McElhone and Davies 1983). The effects of fine sediment on invertebrate production can be dramatic and can cascade to higher trophic levels. For example, the introduction of sand into Hunt Creek, Michigan, resulted in stream aggradation, the replacement of pool and riffles series with continuous run habitat, a large reduction in food for brook trout (*Salvelinus fontinalis*), and a 50% reduction in their numbers (Alexander and Hansen 1986).

Complex habitats often support greater standing crops and production (e.g., Murphy et al. 1984; McMahon and Hartman 1989; Fausch and Northcote 1992) and enhance the growth and survival of stream-dwelling fishes (e.g., Quinn and Peterson 1996; Sundbaum and Näslund 1998). Observational studies indicate that salmonids seek optimal conditions of depth and velocity for foraging, within the constraints of competition (Fausch 1984) and predation (Lima and Dill 1990). Experimental evidence (Fausch (1993) and references therein) suggests that habitat structures provide three main features related to the tradeoffs between foraging and predation risk: (*i*) velocity refuge, (*ii*) visual isolation, and (*iii*) overhead cover. Structures that provide visual isolation from other fish reduce energetically costly agonistic behaviour (Sundbaum and Näslund 1998), and overhead cover such as riparian vegetation can reduce the degree of predator vigilance. Physical habitats that provide velocity refuge, such as boulders, allow fish to hold low-velocity positions adjacent to faster water currents and thus maximize their energy intake from drifting food items while minimizing the cost of swimming to maintain position (Fausch and White 1981; Fausch 1984; McLaughlin and Noakes 1998).

Interestingly, the size and composition of invertebrates in the diets of YOY grayling in the natural and artificial streams reveal little if any difference, despite poor growth in the artificial stream. This similarity of stomach contents contrasts with the differences in the invertebrate prey base and suggests that grayling in the artificial stream may have to expend more energy in obtaining their food requirements, ultimately resulting in a lower net gain in energy and poor growth. Our sensitivity analyses of the bioenergetics model indicated that a 50% increase in the activity multiplier resulted in a twofold reduction in body mass and suggests that increased swimming costs could contribute to the observed differences in growth between the artificial and natural streams. Still, the model was almost twice as sensitive to changes in food consumption (*P* value).

Perspective

The compensation of habitat in the artificial stream has been neither a success nor a failure; instead, there has been a progression of successes necessary for compensation. In this hierarchical framework, the artificial stream allows grayling to migrate through and spawn in it and the eggs to hatch; however, as nursery habitat, it offers cooler temperatures, low invertebrate production, and physically simple habitat and as a result produces relatively small YOY, even though fish densities in the artificial stream are lower than those observed in natural streams. Temperature effects appear limited, and although habitat complexity may have an influence on the overall productivity, it is doubtful that grayling growth would achieve the levels observed in reference streams if complexity alone were increased in the artificial stream. Rather, we suggest that the scarcity of organic matter in the artificial stream is primarily limiting the overall growth and productivity of benthic invertebrates, ultimately leading to poor growth and production of YOY Arctic grayling. Importantly, DFO's (1986, p. 28) definition of productive capacity explicitly acknowledges the importance of food and trophic interactions. This differs from many traditional stream habitat management plans in which managers typically focus on modification of the physical structure of streams via instream habitat structures, without much consideration of the flow of energy and nutrients. We strongly urge habitat managers to use all available knowledge to design compensation programs, not just a physical perspective. Some of the problems associated with the artificial stream most likely could have been predicted from an understanding of stream ecosystem ecology.

The growth of young fish can have significant implications at the population level and thus directly affect the productive capacity of an ecosystem (Holtby 1988). Size-dependent mortality, stemming from overwinter starvation (Post and Evans 1989) and predation (Post et al. 1999), is frequently observed in cohorts of young fish (Miller et al. 1988; Post and Parkinson 2001). For young fish, the chances of an individual surviving a period of low food availability, such as the long arctic winter, is largely based on their energy reserves and the rate at which they are used metabolically. It is thus reasonable to suggest that age-0 grayling in the artificial stream, which have reached an end-of-summer mass approximately half that observed in natural streams, may experience reduced survival during their first winter. In turn, recruitment into the breeding population may be impaired.

As a result of our assessment of fish production and the productive capacity of the artificial stream, managers can begin to make defensible decisions and guide the subsequent work that will be required for compensation. The objectives of future studies will need to consider a number of important questions such as (*i*) what can be done to improve the growth of grayling while continuing to learn about the relative roles of food production, physical habitat, and temperature, (*ii*) at what point will grayling have reached an acceptable rate of growth, (*iii*) because the artificial stream is a completely new ecosystem and ecological succession in the Arctic is slow, how can we speed up the successional process, and (*iv*) how long should compensation take? These questions are challenging, but the characteristics of this ecosystem and the information that our studies have provided offer an unparalleled opportunity to advance the study of fish habitat compensation and stream restoration ecology.

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The power of experiments for estimating relative reproductive success of hatchery-born spawners

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Abstract: An a priori power analysis was conducted to aid the design of experiments aimed at estimating the reproductive success of hatchery-born spawners relative to wild-born spawners using parentage assignment. Power was defined as the probability of rejecting the null hypothesis of equal reproductive contributions of hatchery- and wild-born spawners. A maximum likelihood estimator of relative reproductive success and its variance were derived. The estimator allowed multiple brood years of data, which was an extension of current approaches. Power increased with stock productivity, initial spawner abundance, fraction of recruits and spawners sampled, and the number of brood years examined. Power decreased with error variance used in the production function. Assuming a fixed total number of spawners, power was a concave-down function of the fraction of hatchery-born spawners. Using nominal values of productivity, error variance, and fraction of hatchery-born spawners, an experiment could achieve 0.8 power if it was run for at least 5 years or if it was applied to a stock with high initial female spawners (>200) and run for at least 2 years.

Résumé : Une analyse de puissance a priori a servi à planifier des expériences pour estimer, par détermination de la filiation, le succès de reproducteurs provenant de piscicultures par comparaison à des reproducteurs sauvages. La puissance se définit comme la probabilité de rejeter l'hypothèse nulle que les reproducteurs sauvages et ceux des pisciculture contribuent également à la reproduction. Un estimateur de vraisemblance maximale du succès relatif de la reproduction et de sa variance a été mis au point. L'estimateur permet l'utilisation de données provenant de plusieurs années de reproduction, ce qui est une amélioration des méthodes courantes. La puissance augmente avec la productivité du stock, l'abondance initiale des reproducteurs, la fraction des recrues et des reproducteurs échantillonnée et le nombre d'années de reproduction examiné. La puissance diminue avec la variance d'erreur utilisée dans la fonction de production. Si on assume que le nombre total de reproducteurs est constant, la puissance est une fonction concave décroissante de la fraction de reproducteurs provenant des piscicultures. En utilisant des valeurs nominales de productivité, de variance d'erreur et de fraction de reproducteurs nés en pisciculture, une expérience peut atteindre une puissance de 0,8 si elle couvre au moins 5 années ou si elle implique un stock contenant un nombre initial de reproducteurs élevé (>200) sur une période d'au moins 2 ans.

[Traduit par la Rédaction]

Introduction

The presence of hatchery-born spawners is believed to influence reproductive success on the spawning grounds in many ways, yet its actual effect on recruits per spawner remains one of the greatest unknowns hampering the estimation of long-term population trends of salmonid populations. When hatchery-born fish are allowed to interbreed with wild-born fish on spawning grounds (i.e., the wild population is supplemented), the productivity of naturally spawning populations may be reduced, compromising conservation objectives (Reisenbichler and Rubin 1999). Even if the hatchery spawners did not affect the reproductive success of wild-born spawners, hatchery-born spawners could still hamper the estimation of trends in the wild portion of the population. To see this, suppose that a large total recruitment per wild spawner is evident in the retrospective spawner series. If hatchery-reared spawners are as effective at producing adult progeny as wild fish, then the large total recruitment per wild spawner could have been due to a large input of hatchery-reared spawners one generation ago, even though the trend in wild population abundance was downward. At the other extreme, if hatchery-reared spawners produce no adult progeny (recruits), then a large total recruitment per wild spawner indicates a clear upward trend in wild population abundance. Reliably estimating the relative reproductive success of hatchery-born spawners is also important for evaluating the effectiveness of a captive rearing program as a restoration strategy (Fleming 1994; Berejikian et al. 1997).

Despite its importance, estimates of the relative reproductive success of hatchery-born spawners are scarce, and where these estimates exist, their precision is unreported. Chilcote et al. (1986) used electrophoretic methodologies of Allendorf (1975) to estimate differential reproductive success of hatchery and wild summer-run steelhead (*Oncorhynchus mykiss*) under natural conditions. They concluded that the success of hatchery fish in producing smolt offspring was only 28% that of wild fish. However, standard errors or confidence intervals were lacking, so it is unknown whether this estimate is reliable. Furthermore, their experiments based repro-

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ductive success on smolt offspring per spawner, not adult offspring per spawner, which would have been a superior measure of overall reproductive success. This work was later expanded by Leider et al. (1990), who showed that relative reproductive success of naturally spawning hatchery steelhead compared with wild steelhead decreased from 0.75–0.788 at the subyearling stage to 0.108–0.129 at the adult stage. This suggests that using juvenile progeny to calculate relative reproductive success instead of adult progeny ignores important survival effects.

Among the recent investigations are those of Garant et al. (2001) and Taggart et al. (2001), which use a pedigree analysis whereby parents (spawners) are assigned to offspring (adult returns) using DNA analysis. This approach uses genetic differences among individuals to assess fitness. It differs from the approach of earlier experiments of Reisenbichler and McIntyre (1977), Leider et al. (1990), and Fleming et al. (2000) that used genetic markers that differentiated among groups of spawners, not individuals. The advantage of the group-based approach is that it requires few genetic markers; its disadvantage is that it requires good genetic differentiation between groups and, unlike the individual approach, does not provide individual fitness data, which can be used to estimate fitness with respect to individual traits such as run timing, size, or age (Morgan and Conner 2001). In individual-based experiments, the parents of the adult progeny (recruits) can be uniquely determined with high probability by using microsatellites, which serve as nonlethal, permanent, heritable markers (Ferguson and Danzmann 1998; Bernatchez and Duchesne 2000; Letcher and King 2001). Such experiments are expensive and exacting, requiring a high number of microsatellite loci and alleles per locus for reliable parentage assignment, but they may provide a relatively swift, accurate procedure for estimating the relative reproductive success of hatchery spawners.

Besides those studies referenced above, there are many individual-based experiments on relative reproductive success of hatchery-born spawners now underway. For example, in the Pacific Northwest, such experiments have multiplied, partly because relative reproductive success of hatchery-born spawners has been identified as a critical uncertainty in determining whether escapement goals have been met (National Marine Fisheries Service 2000). These and other experiments will have a higher chance of success (yielding reliable estimates) if they are designed using a priori power analysis (Peterman 1990*a*). An a priori power analysis is conducted before an experiment to determine appropriate sample size (and other design variables) that will successfully reject a null hypothesis when it is untrue. In the context of supplementation, researchers are interested in maximizing the probability of rejecting the null hypothesis that the reproductive successes of hatchery- and wild-born spawners are equal when they are not. This probability is defined as power.

The objective of this paper is to estimate the a priori power of an experiment used to estimate relative reproductive success of hatchery-born spawners, θ, where hatchery-born fish are allowed to spawn naturally with wild-born fish. I developed a likelihood-based, iterative procedure for estimating the relative reproductive success of hatchery-born spawners. This estimator forms the basis for a statistical test of whether recruits per hatchery-born spawner and recruits per wild-born spawner are equal (i.e., $\theta = 1$), which is the null hypothesis used in the power analysis. I then determined how statistical power varied with the length of experiment, schedule of hatchery-born spawner introduction, stock productivity, spawner abundance, interannual variance in production, fraction of spawners and recruits sampled, and true values of θ. The power results can then be used to help select an informative experiment (Walters and Green 1997), which, in this case, would be an experiment that delivered a reliable estimate of relative reproductive success.

Materials and methods

To conduct an a priori power analysis, it is essential to describe the experiment, determine how the parameter of interest (the relative reproductive success of hatchery-born spawners) will be estimated, and develop a simulation model that generates synthetic data that would be collected during the experiment.

Experiment

The experiment analyzed is one that uses a pedigree analysis on a population of salmon that spawns naturally but is supplemented with hatchery-born spawners. Spawners are nonlethally sampled, identified as hatchery-born or wild-born, and their multilocus microsatellite genotypes are determined. Hatchery-born spawners that arrive (or are released) at the spawning grounds during the experiment may mate with wild-born spawners. Adult returns (recruits) from the sampled spawners are also sampled and genotyped. Pedigree analysis is then used to assign recruits to spawning pairs using a program such as PROBMAX (available online at http://www.uoguelph.ca/~rdanzman/software/PROBMAX/; Danzmann 1997). In the base case, it is assumed that parentage assignment is unambiguous, so that each recruit's parents can be uniquely identified. In a sensitivity analysis, however, this assumption is relaxed to see how power changes when only a fraction of the returning spawners are genotyped. The number of loci and alleles per locus sufficient to make the assignment unambiguous (given that both parents were genotyped) can be determined using PROBMAXG (Danzmann 1997).

Estimation

Inferences are made for θ, the relative reproductive success of hatchery-born spawners, which is the mean ratio of recruits per hatchery-born female spawner to recruits per wild-born female spawner. A similar ratio can be defined for male spawners, but for the sake of simplicity, only the female ratio is treated in this paper. The interpretation of θ is straightforward. When $\theta = 0$, no recruits have a hatchery-born parent. When $\theta = 1$, on average, a hatchery-born female spawner produces as many recruits as a wild-born female spawner.

I next derive the likelihood function of θ to obtain a maximum likelihood estimate. Suppose that the expected number of offspring per wild-born mother spawning in brood year t is p_t, so that the expected number of offspring per hatchery-born spawner is θp_t. Then, the probability that a returning individual had a wild-born mother is $S_{W,t}p_t/(S_{W,t}p_t + S_{H,t}p_t\theta)$ and the probability that it had a hatchery-born mother is

$S_{H,t}\theta p_t/(S_{W,t}p_t + S_{H,t}p_t\theta)$, where $S_{W,t}$ is the number of wild-born female spawners and $S_{H,t}$ is the number of hatchery-born female spawners in brood year t. Treating the assignments as independent, the likelihood function, representing the joint probability distribution of the random variables $Z_{i,t}$, where $Z_{i,t} = 1$ if recruit i has a hatchery-born mother and $Z_{i,t} = 0$ if it has a wild-born mother, is given by

$$(1)\qquad L(\theta) = \prod_{t=1}^{n} \frac{(S_{W,t}p_t)^{R_{W,t}}(S_{H,t}\theta p_t)^{R_{H,t}}}{(S_{W,t}p_t + S_{H,t}p_t\theta)^{R_{W,t}+R_{H,t}}} = \prod_{t=1}^{n} \frac{S_{W,t}^{R_{W,t}}\, S_{H,t}^{R_{H,t}}\, \theta^{R_{H,t}}}{(S_{W,t} + S_{H,t}\theta)^{R_{W,t}+R_{H,t}}}$$

where n represents the number of brood years used in the experiment, $R_{H,t}$ is the number recruits (adult progeny) that have a hatchery-born mother, and $R_{W,t}$ is the number of recruits that have a wild-born mother. The likelihood in eq. 1 represents a special case of the likelihoods used by others that express expected recruits per spawner as a log linear function of covariates (Smouse et al. 1999; Morgan and Conner 2001).

The estimator used in this analysis, $\hat{\theta}$, is the maximum likelihood estimator (MLE), which is found by taking the natural log of the likelihood function and then setting the partial derivatives with respect to the parameters equal to zero (see Appendix A). In doing this, one finds that $\hat{\theta}$ satisfies the algebraic equation

$$(2)\qquad \hat{\theta} = \frac{\sum_{t=1}^{n} R_{H,t}}{\sum_{t=1}^{n} S_{H,t}(R_{W,t} + R_{H,t})/(\hat{\theta}S_{H,t} + S_{W,t})}$$

which is solved numerically using a root-finding technique known as the Van Wijngaarder – Dekker – Brent method, which combines root bracketing, bisection, and inverse quadratic interpolation (Brent 1973; Press et al. 1992). When $n = 1$, no numerical method is needed; the estimator is simply $\hat{\theta} = R_{H,1}S_{W,1}/R_{W,1}S_{H,1}$.

To illustrate analytically how power tends to change with the variables of the experiment, I derived the variance of $\hat{\theta}$ using asymptotic maximum likelihood theory. For a fixed value of θ, power tends to increase with precision if bias is well behaved. I derived the variance of $\hat{\theta}$ by inverting the Fisher information (Hogg and Craig 1995), which was calculated as the negative of the expected value of the log likelihood's second derivative (see Appendix A). This yielded

$$(3)\qquad \mathrm{var}(\hat{\theta}) = \left[\sum_{t=1}^{n} \frac{p_t S_{H,t} S_{W,t}}{\theta(S_{W,t} + \theta S_{H,t})}\right]^{-1}$$

which demonstrates that the variance of $\hat{\theta}$ increases with θ, decreases with both $S_{W,t}$ and $S_{H,t}$, and decreases with p_t, which is a measure of stock productivity equaling recruits per wild-born female spawner. Thus, theory shows that greater precision can be obtained when using a stock with high spawner counts and relatively high recruits per spawner. Although the theory provides a useful guide, this paper does not rely on analytical formulas alone because they are asymptotic results, which can be inaccurate, especially at small sample sizes. For better accuracy, Monte Carlo estimates of power were used.

Generating model

Before Monte Carlo estimates of power could be obtained, a simulation model for generating synthetic data sets of recruits and spawners of both hatchery- and wild-born salmon was needed. The maximum likelihood estimator was applied to the synthetic data sets to build an estimate of the sampling distribution of $\hat{\theta}$. The estimate of the sampling distribution was used to estimate power and bias.

First, I describe the simulation of the mating process. For convenience, let WW, WH, HW, and HH represent matings between a wild-born female and wild-born male, wild-born female and hatchery-born male, hatchery-born female and wild-born male, and hatchery-born female and wild-born male, respectively. Assume that there are exactly $S_{W,t}$ wild-born female spawners on the spawning grounds and $S_{H,t}$ hatchery-born female spawners and that the ratio of hatchery-born spawners to wild-born spawners, denoted f, is under experimental control. Also assume equal numbers of wild-born male and female spawners and equal numbers of hatchery-born male and female spawners. Then, because mating is random, the probability that there are exactly x_{WW} matings follows a hypergeometric distribution

$$(4)\qquad \Pr(X_{WW,t} = x_{WW}) = \frac{\binom{S_{W,t}}{x_{WW}}\binom{S_{H,t}}{S_{W,t} - x_{WW}}}{\binom{S_{W,t} + S_{H,t}}{S_{W,t}}}$$

where $X_{WW,t}$ is a random variable representing the number of WW matings, and $x_{WW} = 0, 1, 2, \ldots, S_{W,t}$. The random variables representing the numbers of WH, HW, and HH matings are then $X_{WH,t} = S_{W,t} - X_{WW,t}$, $X_{HW,t} = S_{W,t} - X_{WW,t}$, and $X_{HH,t} = S_{H,t} - S_{W,t} + X_{WW,t}$. Assume that a WW mating produces a mean of q_t recruits, whereas WH, HW, and HH matings produce means of $\beta_{WH}q_t$, $\beta_{HW}q_t$, and $\beta_{HH}q_t$ recruits, respectively. The constants β_{WH}, β_{HW}, and β_{HH} each represent a ratio of recruits per mating (of type WH, HW, and HH, respectively) to recruits per WW mating. In the simulations, the value of q_t followed a Ricker-type production function:

$$(5)\qquad q_t = 2\exp(a - 2b(S_{H,t} + S_{W,t}) + \varepsilon_t)$$

where a is the Ricker density-independent parameter; b is the Ricker density-dependent parameter ($2b$ is used because $S_{H,t} + S_{W,t}$ represents the number of female spawners); and ε_t is a normal error term with mean zero and variance σ^2, capturing the year-to-year variability in recruits per spawner. Although other production functions, such as the Beverton–Holt, could be used instead, the Ricker production function was employed because it is the most commonly used production function in spawner–recruit analysis.

Nominal values of the production function parameters ($a = 1.1062 \times 10^{-2}$, $b = 5.4007 \times 10^{-4}$, and $\sigma^2 = 1.45$) were taken from the Imnaha River stream-type chinook index population of the Snake River, which is being considered for a reproductive success experiment (P. Moran, National Marine Fisheries Service, 2725 Montlake Blvd E., Seattle, WA 98112, personal communication). The recruits for each brood year follow a Poisson process with mean $X_{\mathrm{WW},t}q_t$ for the recruits from a WW mating, and means $X_{\mathrm{WH},t}\beta_{\mathrm{WH}}q_t$, $X_{\mathrm{HW},t}\beta_{\mathrm{HW}}q_t$, and $X_{\mathrm{HH},t}\beta_{\mathrm{HH}}q_t$ for the recruits from WH, HW, and HH matings, respectively.

The power analysis requires the true value of θ in the simulations. The true θ can be determined as a function of β_{WH}, β_{HW}, β_{HH}, and *f*, which is derived using the following four equations:

$$(6)\qquad E\{R_{\mathrm{H},t}/S_{\mathrm{H},t}\} = \frac{(E\{X_{\mathrm{HW},t}\}\beta_{\mathrm{HW}} + E\{X_{\mathrm{HH},t}\}\beta_{\mathrm{HH}})q_t}{S_{\mathrm{H},t}}$$

$$(7)\qquad E\{R_{\mathrm{W},t}/S_{\mathrm{W},t}\} = \frac{(E\{X_{\mathrm{WW},t}\} + E\{X_{\mathrm{WH},t}\}\beta_{\mathrm{WH}})q_t}{S_{\mathrm{W},t}}$$

$$(8)\qquad E\{X_{\mathrm{WW},t}\} = \frac{S_{\mathrm{W},t}^2}{S_{\mathrm{W},t} + S_{\mathrm{H},t}}$$

$$(9)\qquad E\{R_{\mathrm{H},t}/S_{\mathrm{H},t}\} = \theta E\{R_{\mathrm{W},t}/S_{\mathrm{W},t}\}$$

Equations 6 and 7 follow from using expectation of Poisson random variables. Equation 8 follows from expectation of a hypergeometric random variable given by eq. 4. Equation 9 follows by definition of θ. Taken together, these four equations imply

$$(10)\qquad \theta = \frac{(1-f)\beta_{\mathrm{HW}} + f\beta_{\mathrm{HH}}}{1 - f + f\beta_{\mathrm{WH}}}$$

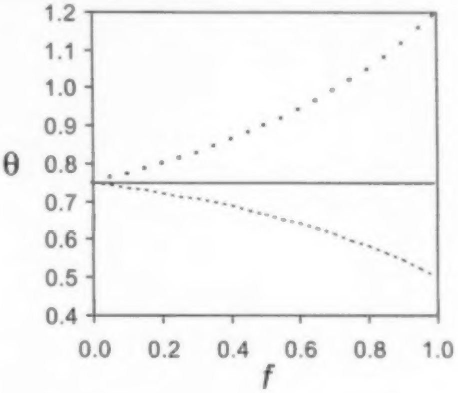
which demonstrates that θ is a function of the fraction of hatchery-born spawners, *f*. Taking the first derivative dθ/d*f* in eq. 10 shows that the relationship between θ and *f* depends critically on the quantity $\beta_{\mathrm{HH}} - \beta_{\mathrm{HW}}\beta_{\mathrm{WH}}$. When $\beta_{\mathrm{HH}} = \beta_{\mathrm{HW}}\beta_{\mathrm{WH}}$ is positive, θ increases with *f*; when it is negative, θ decreases with *f*, when it is zero, θ does not change with *f* (Fig. 1). For the sake of simplicity, I assume that $\beta_{\mathrm{HH}} - \beta_{\mathrm{HW}}\beta_{\mathrm{WH}}$ is zero, so that θ does not depend on *f*, and I assume that $\beta_{\mathrm{HW}} = \beta_{\mathrm{WH}}$. The generating model, however, is entirely general and can accept any values of β_{WH}, β_{HW}, and β_{HH}.

The recruits are distributed over the return years according to a maturity schedule that is randomly sampled from the observed maturity schedules of the Imnaha River index stock during 1978–1994. The maturity schedule determines the contributions of recruits to spawner abundances in subsequent brood years. The simulations are initialized with alternative spawner abundances to see how initial spawners influence power. There were three alternative initial spawner abundances explored, $S_{\mathrm{W},1} + S_{\mathrm{H},1} = 50$, 100, and 200, and in the base case, $f = 0.5$ (i.e., $S_{\mathrm{W},t} = S_{\mathrm{H},t}$).

Power and bias

Statistical power is the probability of rejecting a null hypothesis about the parameter of interest, which in this case is θ. Once the null hypothesis is specified, power is a function of α (type I error), the true parameter, sample size, and the underlying probability model (Peterman 1990*a*, 1990*b*). The null hypothesis used was H_0: θ = 1, representing equal reproductive success of hatchery and wild spawners, against the one-sided alternative H_a: θ < 1. This null hypothesis was untested and treated as true in the works of Kareiva et al. (2000), Deriso et al. (2001), and Peters and Marmorek (2001) when analyzing recruits per spawner of the threatened Snake River stream-type chinook index populations. I calculated power using the usual Neyman–Pearson paradigm of fixing the significance level (α) and choosing a design that makes power sufficiently large. For this analysis, I chose the usual design criteria of α = 0.05 and power at least 0.8. I flagged designs that achieved these criteria when the true value of θ was 0.8, which was an alternative hypothesis proposed by U.S. National Marine Fisheries Service (Cumulative Risk Initiative 2000).

Fig. 1. Reproductive success of hatchery-born female spawners, θ, is depicted as a function of fraction of hatchery-born spawners on the spawning grounds, *f*, under different assumptions about the relative reproductive success of the various crosses (β_{WH}, β_{HW}, β_{HH}). When $\beta_{\mathrm{HH}} - \beta_{\mathrm{HW}}\beta_{\mathrm{WH}}$ is positive, θ increases with *f* (dotted line); when it is negative, θ decreases with *f* (broken line); when it is zero, θ does not change with *f* (solid line). In this illustration, $\beta_{\mathrm{WH}} = 0.5$, $\beta_{\mathrm{HW}} = 0.75$, and $\beta_{\mathrm{HH}} = 0.6$, 0.25, and 0.375 for the increasing, decreasing, and flat relationships between θ and *f*, respectively.



To estimate variance of the estimator and power, the generating model was used to provide *B* = 10 000 synthetic data sets to which the estimator $\hat{\theta}$ was applied. This yielded *B* Monte Carlo replications of the estimator, $\hat{\theta}^{*k}$, $k = 1, 2, \ldots, B$. The critical value, θ_{crit}, was estimated as the 0.05 quantile (corresponding to α = 0.05) of the *B* Monte Carlo replications of $\hat{\theta}$ generated assuming θ = 1. Power associated with each true value of θ used in the simulations was then estimated as the fraction of the replications of $\hat{\theta}$ not exceeding θ_{crit}. This was identical to a bootstrapping approach (Efron and Tibshirani 1993), except that the synthetic data sets were not generated by resampling data but by sampling a parametric probability model. To determine the number of years of experimentation needed to obtain high power, I calculated power for *n* = 1, 2, 5, and 10.

As another important measure of the accuracy of $\hat{\theta}$, bias was also estimated. Bias measures the difference between the expectation of the estimator $\hat{\theta}$ and the true value of θ. If the expectation of $\hat{\theta}$ is far from θ, this reveals an important inaccuracy, which ought to be remedied through a bias correction procedure. The estimate of bias that I used was

Table 1. Power values for alternative assumptions.

Sensitivity type	Alternative assumption	$n = 1$	$n = 2$	$n = 5$	$n = 10$
Base case	Base-case assumptions	0.34	0.84	0.99	1.00
Productivity	$a + \ln(0.5)$	0.15	0.34	0.88	0.98
	$a + \ln(2)$	0.79	0.98	1.00	1.00
Error variance	$0.5\sigma^2$	0.49	0.84	0.99	1.00
	$1.5\sigma^2$	0.24	0.81	0.99	1.00
Fraction hatchery spawners	0.10	0.09	0.20	0.71	0.95
	0.25	0.16	0.59	0.97	1.00
	0.75	0.42	0.85	0.99	1.00
	0.90	0.20	0.59	0.96	1.00
Fraction spawners and recruits sampled	0.50	0.14	0.30	0.79	0.97
	0.75	0.20	0.63	0.96	1.00
	0.90	0.26	0.76	0.99	1.00

Note: Here, power is the probability of rejecting the null hypothesis of $\theta = 1$ against the alternative hypothesis $\theta < 1$ when $\alpha = 0.05$ and the true value of θ is 0.8. In the base case, productivity is $a = 1.1062 \times 10^{-2}$, error variance is $\sigma^2 = 1.45$, fraction of hatchery spawners is 0.5, the fraction of spawners sampled is 1, and the initial number of female spawners is 100.

$$\text{bias}(\hat{\theta}) = \hat{\theta}^*(\cdot) - \theta \tag{11}$$

where $\hat{\theta}^*(\cdot) = \sum_{k=1}^{B} \hat{\theta}^{*k}/B$. Bias is usually considered large when it exceeds 25% of the estimator's standard error (Efron and Tibshirani 1993). The Monte Carlo estimate of standard error was

$$\text{SE}(\hat{\theta}) = \left\{ \sum_{k=1}^{B} [\hat{\theta}^{*k} - \hat{\theta}^*(\cdot)]^2/(B-1) \right\}^{1/2} \tag{12}$$

It has been argued that confidence interval width (which depends directly on SE (standard error) and significance level) is a good measure "power" that can replace the traditional measure of power (Stewart-Oaten 1995). This alternative definition of power, however does not take into account the null hypothesis (in this case, the equal reproductive success of hatchery- and wild-born spawners) that experimenters set out to test.

Alternative assumptions

To identify assumptions that influenced power, I conducted several sensitivity analyses that compared power under a set of base case assumptions (described above) with power under alternative assumptions. In each of these sensitivity runs, power was the probability of rejecting the null hypothesis $\theta = 1$, when there were 100 initial female spawners, the true relative reproductive success was $\theta = 0.8$, and the fraction of hatchery-origin spawners was $f = 0.5$.

Productivity

The Ricker *a* parameter, a measure of stock productivity, was varied. A stock with poor productivity was simulated by adding ln(0.5) (a negative number) to the Ricker *a*; a stock with high productivity was simulated by adding ln(2) to the Ricker *a*. These alternatives represented a halving and a doubling of the base case recruits per spawner, respectively.

Error variance

In the base case, I assumed that error variance was $\sigma^2 = 1.45$, which is fairly large compared with other fish populations (Hinrichsen 2001). The alternative error variances explored were $0.5\sigma^2$ and $1.5\sigma^2$.

Fraction hatchery spawners

In the base case, the fraction of hatchery spawners was assumed to be 0.5. Alternative values explored were 0.10, 0.25, 0.75, and 0.90.

Incomplete sampling

If some of the spawners and recruits are not sampled, perhaps because of a damaged weir or budget constraints limiting the number of samples, then there would be adult progeny for which mothers or fathers could not be identified. To gauge the effect of this incomplete sampling on power, I examined how power changed when the fraction of spawners and recruits sampled was less than 1.0. Alternative values explored were 0.50, 0.75, and 0.90.

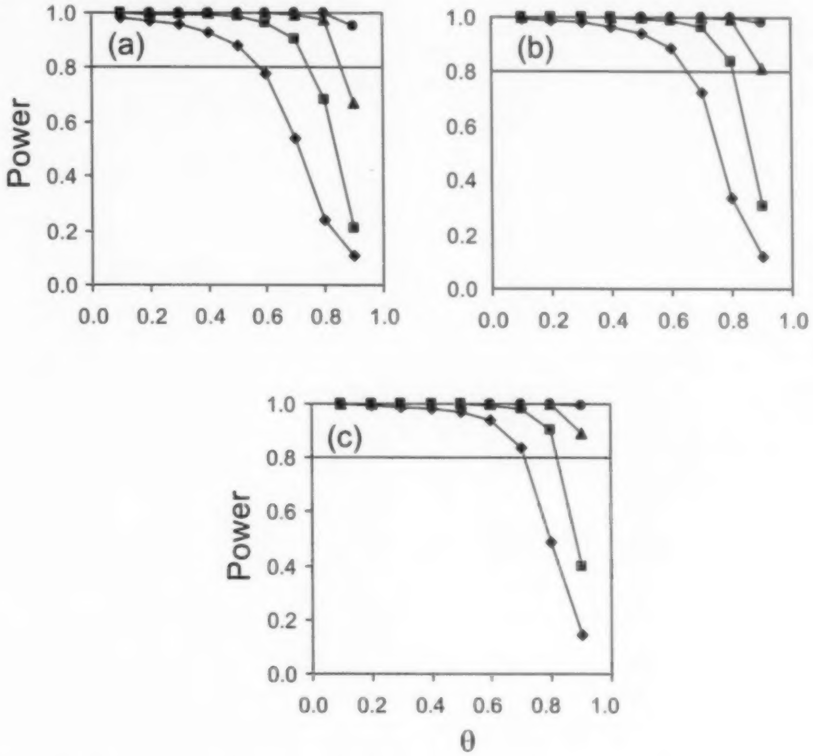
Results

Power and bias

The analysis demonstrated that power increases with initial spawner abundance and years of experimentation, and it decreases with the true value of θ (Fig. 2). For base case assumptions, if one desires power exceeding 0.8 when the true value of θ is 0.8 then are two possibilities: run the experiment for at least 5 brood years or choose a stock with high initial spawners (>100) and run the experiment for 2 years. When the true value of θ is lower than 0.8, then power of 0.8 can be achieved in fewer years. This occurs, naturally, because the null hypothesis was $\theta = 1$. The further the true θ is from 1, the more likely the null hypothesis will be rejected, and hence, the greater the power.

In all simulations, bias was generally upward. It averaged about 3% SE and never rose above 10% SE. Bias was considered small because it did not rise above the cutoff 25% SE in absolute value. Bias decreased with the number of years of experimentation, *n*, falling from an average of 10%

Fig. 2. Power is depicted as a function of true reproductive success of hatchery-born spawners, θ, when the initial female spawners abundance is (*a*) 50, (*b*) 100, and (*c*) 200. Each plot contains power curves when the experiment lasts for 1 year (diamonds), 2 years (squares), 5 years (triangles), and 10 years (circles). Here, power is the probability of rejecting the null hypothesis $\theta = 1$ against the alternative hypothesis $\theta < 1$ with $\alpha = 0.05$. The horizontal line near the top of each plot indicates the power level of 0.8; above this level, power is usually considered sufficiently high.



to 5% SE as n increased from 1 to 10. Bias also decreased with initial number of spawners, falling from an average of 8% to –2% SE as initial female spawners increased from 50 to 200. Although bias was small, it tended to make power estimates slightly too low. This occurred because the bias was often upward, which tended to make the estimate closer to the null hypothesis of $\theta = 1$.

Alternative assumptions

The alternative assumptions used for productivity, error variance, fraction of hatchery spawners, and fraction of spawners sampled all had important effects on power (Table 1). Recall that for the sensitivity analysis, power was defined as the probability of rejecting the null hypothesis $\theta = 1$ when the true value of θ was 0.8 and when the initial female spawner abundance was 100. Power increased with Ricker a (productivity) and fraction of spawners sampled and decreased with error variance.

Power did not change monotonically with fraction of hatchery spawners. Power was a concave-down function of fraction of hatchery-born spawners, f. When f was 0.75, power was maximal, but when the fraction of hatchery spawners was either up at 0.90 or below 0.25, power dropped. This agreed with eq. 3, which shows that the variance of $\hat{\theta}$ is a concave-up function of f.

Discussion

The power analysis suggests that reliably estimating reproductive success of hatchery-born spawners relative to their wild-born counterparts is possible with just a few brood years of spawner–recruit data, and that choosing a population that has large spawner numbers and high productivity may decrease the number of brood years required. These results bode well for experiments now underway and suggest ways in which future experiments can be improved to increase the reliability of estimates of relative reproductive success.

There are, however, some ways in which this analysis may present power values that are higher than those seen in an experiment. Some of these were explicitly treated in the sensitivity analysis, and others were not. One important assumption was that the mean relative reproductive success of hatchery-born spawners would remain constant during studies with multiple years. This would not hold if, for example, fitness of the wild-born spawners decreased because of changes in life-history parameters as they interbreed with hatchery-born spawners (Reisenbichler 1996; Unwin and Glova 1997; Heath et al. 2003) or if the relative fitness of hatchery fish was environmentally dependent: in good years or under low-density conditions hatchery-born fish are likely to have higher relative reproductive success (e.g., Fleming and Gross 1994). Consequently, there may be important changes in mean relative reproductive success of hatchery-born spawners over time that make it necessary to estimate a different θ each year of study (i.e., we would estimate θ_t, $t = 1, 2, \ldots, n$) or to model the change explicitly; in either case, power would decrease. Changes in relative reproductive success over time would also mean that recent estimates can not be used to unmask past trends in the wild-born spawners. This would make futile attempts by the Cumulative Risk Initiative (2000) and others to resolve a trend in wild-born spawners from retrospective data.

Another assumption, mainly for convenience, was that the means of the reproductive success of matings gave a value of θ that did not depend on the fraction of hatchery-born fish, f. As a consequence, hatchery × wild hybrids have higher reproductive success than hatchery × hatchery crosses. This is consistent with Reisenbichler and McIntyre (1977), who found that steelhead fry that were hatchery × wild hybrids had higher survival in streams than hatchery × hatchery crosses. Other assumptions are possible, however, and varying the reproductive success of the various crosses will influence the relationship between fraction of hatchery-born fish, f, and θ as described in eq. 10 and will, in turn, influence power and the optimal choice of f in an experimental design.

Are the experiments underway yielding the appropriate measure of reproductive success of hatchery-born spawners? In all experiments of which I am aware for salmon populations (including the experiment analyzed in this paper), relative reproductive success of hatchery-born spawners is not measured against reproductive success of wild-born spawners without supplementation, which, I believe, is the appropriate baseline. This is the baseline necessary to understand how a population would perform in the absence of supplementation. As it is, if θ is nearly one, one ought not conclude that reproductive success of hatchery-born spawners is nearly equal to that of wild-born spawners in the absence of supplementation: as illustrated in Fig. 1, θ can be inflated owing to supplementation itself, which can lower the reproductive success of the wild-born females. This difficulty can be remedied by using a control stream in which only wild-born adults would be allowed to spawn. The productivity of the supplemented population could then be compared with the productivity of wild-born spawners in the absence of supplementation. Less ideally, if control streams are unavailable, reproductive success of wild-born females could be expressed as a function of f in a regression context. This would require designing an experiment in which f would be varied from year to year to obtain the contrast necessary to estimate regression coefficients. The baseline of reproductive success of wild-born spawners could then be estimated by setting f equal to zero in the estimated regression equation. However, the high variability in recruits per spawner often found in fish populations may make such an approach unreliable in the time frames explored in this paper.

Future power analyses would benefit from improving the underlying probability model as data from relative reproductive success experiments become available. At this point, unfortunately, we do not have the data available to use a simulation procedure that resamples real data (bootstrapping) rather than generating synthetic data sets based on a poorly understood underlying process. As data are collected and analyzed in the numerous experiments now being carried out, bootstrapping can be employed and simulations of the underlying survival and reproductive processes can be refined.

A useful extension of the methods described here would be to express reproductive success as a function of certain covariates associated with individual spawners in a regression. This may reveal important selection gradients in salmon populations that deepen our scientific understanding of reproductive success while increasing the explanatory power of our models. In this context, the origin (hatchery or wild) becomes a factor variable, and other explanatory variables, such as size, age, or time of return, could be incorporated. This regression approach, developed by Smouse et al. (1999) for studying differing male reproductive contributions in a plant population (*Chamaelirium luteum*) is currently being applied to Minter Creek coho (M.J. Ford, National Marine Fisheries Service, 2725 Montlake Blvd E, Seattle, WA 98112, personal communication). Fleming and Gross (1994) used a regression to investigate the effects of competition and several morphological characters on reproductive success of spawners in experimental arenas constructed within a stream channel. Such work can be extended to a more natural setting, making it more representative of supplementation in the wild.

The next phase of this research should proceed by weighing the power (opportunity to learn) of the proposed experiments against their costs. The idea is to select the least expensive design among those that will likely yield reliable results. The important decision variables to consider in the trade-offs between power and cost are: stock chosen for experiment (this determines initial population size, productivity, and error variance), duration of experiment, number of hatchery-born spawners introduced to the spawning grounds, and fraction of spawning population sampled. Although it is clear what design choices will increase power (e.g., choosing a productive, abundant stock), the choices yielding greater power may prove more costly or may simply prove infeasible.

Experiments should be extended to a regional scale that includes many salmonid populations, allowing a more broad assessment of relative reproductive success over many species and areas. For example, in the Columbia Basin, because of the importance that the National Marine Fisheries Service has placed on evaluating supplementation, there is an opportunity to study relative reproductive success in different Pacific salmon species across a broad geographical area under different supplementation strategies. The National Marine Fisheries Service biological opinion has called for conducting two to four studies for each evolutionarily significant unit listed under the U.S. Endangered Species Act (National Marine Fisheries Service 2000). If done properly, such a broad study would allow us to examine how reproductive success varies across species, area, and supplementation strategy. If this research is conducted haphazardly, without good top-down coordination among researchers, an important opportunity to learn will be missed. Without a good probability-based site sampling scheme (such as a stratified random sample), valid statistical inferences cannot be drawn on relative reproductive success over complete set of supplemented endangered salmon populations in the Columbia basin. A coordinated, broad-scale design will be aided by careful consideration of power and how it is affected by the design variables identified in this paper. The design variables (e.g., number of brood years, fraction of spawners hatchery-born) can be selected to sharpen relative reproductive success estimates.

Despite the fact that extensions are needed, I believe that this power analysis has proven valuable. It yielded an estimate of relative reproductive success of hatchery-born spawners that can accommodate multiple brood years of spawner–recruit data, variance formulas for this estimator, the identification of design variables that can be chosen to improve the reliability of the experiment, and upper bounds on the power that can be reasonably obtained in a field experiment. These results can be used as a guide to designing future experiments that will improve the prospects for obtaining useful estimates of relative reproductive success of hatchery-born spawners.

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Appendix A

The derivations of the maximum likelihood estimator of θ and its variance are detailed below. Using maximum likelihood theory, we derive the parameter estimate by setting to zero the partial derivative of ln(*L*) with respect to θ. This yields the equation

$$\text{(A1)}\quad \frac{\partial \ln(L)}{\partial\theta} = \sum_{t=1}^{n} \frac{R_{\mathrm{H},t}}{\theta} - \sum_{t=1}^{n} \frac{S_{\mathrm{H},t}(R_{\mathrm{W},t} + R_{\mathrm{H},t})}{(S_{\mathrm{W},t} + S_{\mathrm{H},t}\theta)} = 0$$

Evaluating eq. A1 at $\hat{\theta}$ and rearranging yields

$$\text{(A2)}\quad \hat{\theta} = \frac{\sum_{t=1}^{n} R_{\mathrm{H},t}}{\sum_{t=1}^{n} S_{\mathrm{H},t}(R_{\mathrm{W},t} + R_{\mathrm{H},t})/(\hat{\theta}S_{\mathrm{H},t} + S_{\mathrm{W},t})}$$

In the special case where $n = 1$, eq. A2 becomes

$$\text{(A3)}\quad \hat{\theta} = (R_{\mathrm{H},1}/S_{\mathrm{H},1})/(R_{\mathrm{W},1}/S_{\mathrm{W},1})$$

The variance of $\hat{\theta}$ is derived by inverting the Fisher information, which is

$$\begin{aligned}
\text{(A4)}\quad -E\left\{\frac{\partial^2 \ln(L)}{\partial\theta^2}\right\}
&= \sum_{i=t}^{n}\left[\frac{E\{R_{\mathrm{H},t}\}}{\theta^2} - \frac{E\{R_{\mathrm{W},t} + R_{\mathrm{H},t}\}S_{\mathrm{H},t}^2}{(S_{\mathrm{W},t} + \theta S_{\mathrm{H},t})^2}\right] \\
&= \sum_{t=1}^{n}\left[\frac{S_{\mathrm{H},t}\theta p_t}{\theta^2} - \frac{(S_{\mathrm{W},t}p_t + S_{\mathrm{H},t}\theta p_t)S_{\mathrm{H},t}^2}{(S_{\mathrm{W},t} + \theta S_{\mathrm{H},t})^2}\right] \\
&= \sum_{t=1}^{n} p_t\left[\frac{S_{\mathrm{H},t}}{\theta} - \frac{S_{\mathrm{H},t}^2}{(S_{\mathrm{W},t} + \theta S_{\mathrm{H},t})}\right] \\
&= \sum_{t=1}^{n} p_t\left[\frac{S_{\mathrm{H},t}(S_{\mathrm{W},t} + \theta S_{\mathrm{H},t}) - \theta S_{\mathrm{H},t}^2}{\theta(S_{\mathrm{W},t} + \theta S_{\mathrm{H},t})}\right] \\
&= \sum_{t=1}^{n} \frac{p_t S_{\mathrm{H},t} S_{\mathrm{W},t}}{\theta(S_{\mathrm{W},t} + \theta S_{\mathrm{H},t})}
\end{aligned}$$

where $E\{\cdot\}$is expectation. Inverting this expression yields the variance formula

$$\text{(A5)}\quad \mathrm{var}(\hat{\theta}\ ) = \left[\sum_{t=1}^{n} \frac{p_t S_{\mathrm{H},t} S_{\mathrm{W},t}}{\theta(S_{\mathrm{W},t} + \theta S_{\mathrm{H},t})}\right]^{-1}$$

Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment

Lisa L. Etherington and David B. Eggleston

Abstract: We assessed determinants and consequences of multistage dispersal on spatial recruitment of the blue crab, *Callinectes sapidus*, within the Croatan, Albemarle, Pamlico Estuarine System (CAPES), North Carolina, U.S.A. Large-scale sampling of early juvenile crabs over 4 years indicated that spatial abundance patterns were size-dependent and resulted from primary post-larval dispersal (pre-settlement) and secondary juvenile dispersal (early post-settlement). In general, primary dispersal led to high abundances within more seaward habitats, whereas secondary dispersal (which was relatively consistent) expanded the distribution of juveniles, potentially increasing the estuarine nursery capacity. There were strong relationships between juvenile crab density and specific wind characteristics; however, these patterns were spatially explicit. Various physical processes (e.g., seasonal wind events, timing and magnitude of tropical cyclones) interacted to influence dispersal during multiple stages and determined crab recruitment patterns. Our results suggest that the nursery value of different habitats is highly dependent on the dispersal potential (primary and secondary dispersal) to and from these areas, which is largely determined by the relative position of habitats within the estuarine landscape.

Résumé : Notre étude porte sur les facteurs déterminants et les conséquences de la dispersion en plusieurs étapes sur le recrutement du crabe bleu, *Callinectes sapidus*, dans le système estuarien Croatan-Albemarle-Pamlico (CAPES) de la Caroline du Nord, É.-U. Un échantillonnage à grande échelle des jeunes crabes immatures pendant 4 ans a révélé que les patterns d'abondance spatiale sont reliés à la taille et sont causés principalement par une dispersion primaire des postlarves (avant l'établissement) et une dispersion secondaire des jeunes (tôt après l'établissement). En général, la dispersion primaire entraîne des abondances élevées dans les habitats situés plus vers la haute-mer, alors que la dispersion secondaire (qui est relativement constante) accroît la répartition des jeunes et augmente potentiellement la capacité de nursery de l'estuaire. Il y a de fortes relations entre la dispersion des jeunes crabes et certaines caractéristiques particulières du vent; cependant, ces patterns varient de façon nette selon les endroits. De nombreux processus physiques (e.g., épisodes de vents saisonniers, calendrier et importance des cyclones tropicaux) influencent par leur interaction les diverses étapes de la dispersion et déterminent les patterns de recrutement des crabes. Nos données laissent croire que la valeur des différents habitats comme nurseries dépend fortement du potentiel de dispersion (primaire et secondaire) vers ces régions ou à partir de ces régions, ce qui est en grande partie déterminé par la position relative des habitats dans le paysage estuarien.

[Traduit par la Rédaction]

Introduction

Dispersal is a key element to understanding abundance patterns and population dynamics of organisms in spatially heterogeneous landscapes (Kareiva 1990; Wiens 1995). Exchange of individuals between groups can have various ecological impacts including increased flow of genetic information, enhanced metapopulation persistence, altered predator–prey dynamics, or modified population distribution and abundance patterns (Stenseth and Lidicker 1992; Dieckmann et al. 1999). Strong connectivity between groups through dispersal implies that local populations are partly dependent on processes occurring outside of the local environment (Caswell 1978; Roberts 1997). Thus, dispersal properties of organisms in spatially heterogeneous landscapes determine the scales at which processes act to control distribution and abundance patterns and population dynamics and the appropriate spatial configuration of conservation efforts (Crowder et al. 2000).

Dispersal properties of an organism are a function of the behavioral and morphological characteristics of the individual, as well as the characteristics of the environment. The degree of connectivity between isolated groups of individuals will be dependent on the life-history strategy of a given species (Horn 1983; Palmer et al. 1996) and the overall dispersal capabilities of the organism. Connectivity between habitat patches could occur during a limited period in the organism's life cycle (e.g., larval phase), or instead, large-scale dispersal may occur during multiple stages. For benthic marine species with open populations (i.e., where local recruitment is uncoupled from local reproduction by a dispersive larval stage; Caley et al. 1996), the importance of dispersal

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in determining population distribution and abundance has often been emphasized in the larval stages, before benthic settlement. There has been a relative lack of attention given to the role of dispersal of juveniles in the post-settlement phase and how this dispersal can influence local and regional population dynamics (Palmer et al. 1996). Nevertheless, there is a growing body of evidence demonstrating the importance of post-settlement dispersal in determining distribution and abundance patterns of diverse taxa including macrofaunal invertebrates (e.g., mollusks, crustaceans, and polychaetes; review by Gunther 1992), reef fish (Robertson 1988; Lewis 1997; Ault and Johnson 1998), and meiofauna (review by Palmer 1988). Post-settlement planktonic dispersal of early juvenile blue crabs (*Callinectes sapidus*) links spatially separated groups of organisms within the estuarine landscape and could be a key determinant of crab distribution and abundance patterns and population dynamics (Etherington and Eggleston 2000).

Patches of habitat can vary in their nursery value for a particular species because of differences in the their spatial pattern (e.g., habitat size, shape, fragmentation, connectivity), as well as their relative location (e.g., to larval supply, other juvenile habitats, or adult habitats; Beck et al. 2001). The relative position of a habitat within a landscape can influence its dispersal potential (both to and from a habitat; e.g., Stockhausen and Lipcius 2003) and therefore is crucial in defining which habitats are the most critical nursery areas requiring conservation. To determine the value of a particular habitat necessitates an understanding of how dispersal at multiple stages influences population abundance and distribution on various spatial and temporal scales.

The current study was conducted to determine how dispersal during multiple stages (both primary dispersal of post-larvae before settlement and secondary dispersal of juveniles soon after benthic settlement) interacts to determine distribution and abundance patterns of a marine invertebrate, the blue crab, within an estuarine landscape. Blue crab recruitment was examined within the Croatan, Albemarle, Pamlico Estuarine System (CAPES), North Carolina, U.S.A. (Fig. 1). The CAPES has two relatively isolated regions of shallow-water, structured habitats, differing in their proximity to oceanic larvae, that could serve as nursery habitats for blue crabs. A conceptual model was proposed by Etherington and Eggleston (2000) whereby, in the absence of tropical cyclones, post-larval blue crabs settle within the seagrass beds near the inlets of the CAPES (Fig. 1) and later disperse to more inland portions of the estuary either via the water column as early juveniles or through benthic dispersal as later-stage juveniles. We predicted that tropical cyclones could increase the nursery capacity of the estuarine system by delivering post-larvae to the sound region of the estuary, as well as facilitating juvenile post-settlement dispersal to areas that do not normally experience consistent settlement of post-larvae (Etherington and Eggleston 2000; D. Eggleston, unpublished data). The present study was conducted to test this model of blue crab recruitment over several years containing different patterns of tropical cyclone frequency to better understand the determinants of pre- (primary) and post-settlement (secondary) dispersal and the implications of this multistage dispersal on spatial dynamics of recruitment within the estuarine landscape.

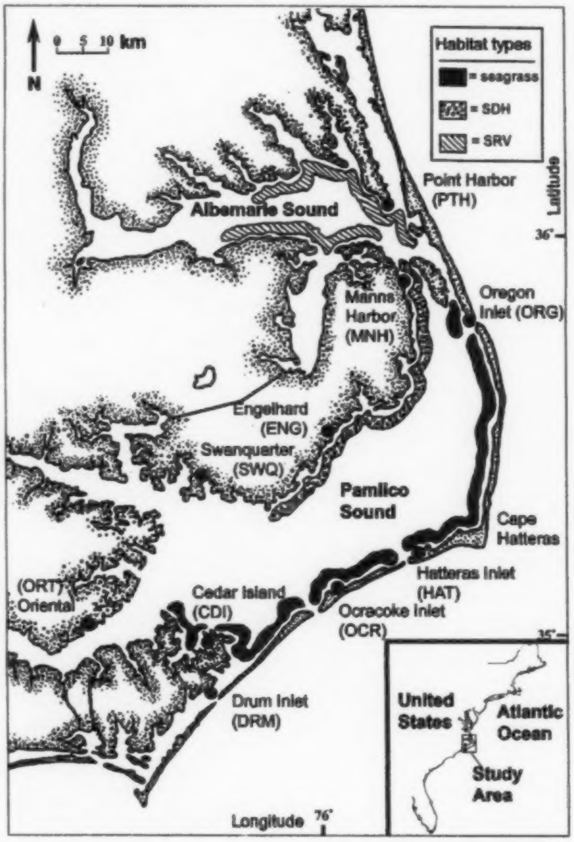


Fig. 1. The Croatan, Albemarle, Pamlico Estuarine System (CAPES) in North Carolina, U.S.A., including all sites that were sampled for juvenile blue crab (*Callinectes sapidus*) density. Inlet sites: Oregon Inlet (ORG), Hatteras Inlet (HAT), Ocracoke Inlet (OCR), and Drum Inlet (DRM). Sound sites: Point Harbor (PTH), Manns Harbor (MNH), Engelhard (ENG), Swanquarter (SWQ), Cedar Island (CDI), and Oriental (ORT). Complex habitat types present in the CAPES: seagrass, shallow detrital habitat (SDH), and submersed rooted vasculars (SRV; primarily, *Myriophyllum spicatum*).

Our examination of juvenile blue crab recruitment dynamics within North Carolina focused on three main issues: (*i*) temporal variation in size-specific juvenile abundance in spatially separated estuarine regions; (*ii*) influence of wind forcing on multistage crab dispersal and subsequent initial and secondary recruitment; and (*iii*) spatial and temporal occurrence of post-settlement planktonic dispersal and its relationship with tropical cyclones.

Methods

Blue crab life history

The blue crab exhibits a complex life cycle whereby larval and post-larval stages reside in an oceanic environment, whereas juvenile and adults have a benthic existence, primarily in estuarine habitats. Mature females with egg masses migrate from lower salinity estuarine habitats towards oceanic waters where they release their larvae at the bay mouth or inlets (Van Engel 1958; Williams 1984). Larvae spend ~30 days in the oceanic environment before metamorphosing to the post-larval stage (McConaugha et al. 1983). Post-larvae then move back into the estuary using a combination of physical forcing mechanisms such as wind-driven surface currents and tidal currents (Epifanio et al. 1984; Goodrich et al. 1989). Once within the estuarine environment, post-larvae settle within complex benthic habitats such as seagrass (e.g., Heck and Thoman 1981; Orth and van Montfrans 1987), salt marsh (Thomas et al. 1990), or shallow detrital habitats (Etherington and Eggleston 2000) before metamorphosing to the first benthic juvenile stage (J1). Juvenile instars (molting stages) will subsequently be referred to as J1, J2, J3, etc.

Post-settlement planktonic dispersal of juvenile blue crabs from within seagrass beds has been documented in both field (Etherington and Eggleston 2000; Blackmon and Eggleston 2001) and laboratory studies (Blackmon and Eggleston 2001). This secondary juvenile dispersal appears to be an active behavior, primarily in response to increasing current speeds (Blackmon and Eggleston 2001) and induced by interactions between juveniles within seagrass beds (Etherington et al. 2003). Patterns of juvenile abundance indicative of post-settlement planktonic juvenile dispersal have been observed over large spatial scales (up to 50 km) in the CAPES (Fig. 1). Evidence of juvenile blue crabs within the water column away from structured habitats supports this notion of large-scale dispersal (Mense and Wenner 1989; N. Reyns, Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, unpublished data). Thus, post-settlement planktonic juvenile dispersal has the potential to link groups of organisms that would otherwise be spatially separated (because of the amount of time that it would take juveniles to walk a great distance or because of unfavorable conditions such as a lack of refuge or an abundance of predators between habitat patches; Etherington and Eggleston 2000). Juvenile patterns representative of post-settlement planktonic dispersal of juvenile blue crabs have been documented during time periods associated with tropical cyclones (Etherington and Eggleston 2000). It is possible that this secondary dispersal only occurs during strong physical forcing events within the estuary, or instead, juvenile dispersal could be associated with a variety of environmental conditions.

Study system and sampling sites

We chose to examine recruitment of a marine benthic invertebrate to spatially isolated habitats within a large, primarily wind-driven estuary, the CAPES, North Carolina, U.S.A. (Fig. 1). The CAPES is a shallow lagoonal system that is enclosed by a strip of barrier islands, the Outer Banks. These physical attributes cause circulation within the system to be primarily driven by winds, with tidal influence only prevalent within 3–5 km of the inlets (Pietrafesa and Janowitz 1991; Tom Hopkins, Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, personal communication). Therefore, different physical forcing mechanisms predominate in different regions of the estuarine system and could influence transport of post-larval and juvenile crabs.

We divided the CAPES into two main regions, inlet and sound, to define differences in proximity to oceanic sources of post-larval blue crabs. Within the inlet region, we identified four sites: Oregon Inlet, Hatteras Inlet, Ocracoke Inlet, and Drum Inlet (Fig. 1). The sound region consists of six sites that were distributed along the interior of the estuarine system: Point Harbor, Manns Harbor, Engelhard, Swanquarter, Oriental, and Cedar Island (Fig. 1). Overall, we had relatively wide sampling coverage of the CAPES, with sites located between 15 and 50 km apart along ~300 km of shoreline.

Spatial and temporal variation in crab abundance patterns

Juvenile sampling

Sampling of juvenile blue crabs consisted of replicated standardized suction sampling of a 1.674-m^2 area within a given structured benthic habitat (see Etherington and Eggleston (2000) for details). Habitat types varied across sites; most sites contained seagrass (*Zostera marina*, *Halodule wrightii*, and *Ruppia marina*), but some sites contained primarily shallow detrital habitats (SDH) and others were dominated by the freshwater macrophyte *Myriophyllum spicatum*, which we have categorized as SRV (submersed rooted vasculars, Fig. 1; Etherington and Eggleston 2000). Samples were taken from the complex habitat that was available at each site; densities of juvenile blue crabs do not differ significantly between these complex habitat types (Etherington and Eggleston 2000). Samples were taken at each site within a 5-day period beginning 3 days after the new moon in the months of August, September, and October in the years 1996–1999. Two sites were removed from the sampling protocol in 1998 (Oriental and Cedar Island) based on consistently low juvenile abundance, and one site was added to the sampling scheme in 1998 (Drum Inlet) to improve spatial coverage within the southern portion of the system. A core set of seven sites spanning the inlet and sound regions was sampled consistently over the 4-year period. Six replicate samples were taken at each site during a time period; however, the number of samples that were sorted in the laboratory ranged from 3 to 6 in an effort to reduce the amount of sorting time where categories had low variance between samples or extremely low numbers of juveniles (see Etherington and Eggleston (2000) for examples of sample size reduction and justification). From these samples, we quantified the density of juvenile instars 1 and 2 (J1–J2; carapace width 2.2–4.2 mm; 0–16 days since settlement) and the density of juvenile instars 3 through 5 (J3–J5; carapace width 4.3–9.1 mm; 14–46 days since settlement) (Etherington and Eggleston 2000). These size classes were chosen because (*i*) spatiotemporal patterns of J1–J2 recruitment are similar to patterns of post-larval settlement (measured with artificial settlement substrates; D. Eggleston, unpublished data); therefore, J1–J2 stages likely reflect processes influencing post-larval delivery and settlement; and (*ii*) post-settlement planktonic dispersal has been detected between J1–J2 and J5 stages (Etherington and Eggleston 2000); thus, patterns of distribution and abundance of J3–J5 stages are influenced by post-settlement juvenile dispersal. Thus, patterns of J1–J2 abundance are a reflection of primary dispersal occurring during the post-larval stage (pre-settlement), whereas J3–J5 abundance patterns incorporate the process of secondary dispersal by early post-settlement juveniles.

Statistical analyses

To examine spatial and temporal patterns of juvenile recruitment, we used a repeated-measures ANOVA (analysis of variance) model with month (August, September, October) as the within-subject factor and year (1996, 1997, 1998, 1999) and region (inlet, sound) as between-subject factors. Because a site was repeatedly sampled throughout a recruitment season, the repeated-measures design accounted for correlation in juvenile density between sampling months. Recruitment values between years were considered independent of one another; therefore, we blocked by year. We were primarily interested in spatial differences between regions (inlet and sound); therefore, we nested site within region. Significant interaction effects were interpreted with Ryan's Q multiple-comparison tests and lower-level ANOVA models.

Relationship between blue crab recruitment and wind components

Classification of wind

Wind data for Cape Hatteras National Weather Service Office (located at Cape Hatteras, N.C.; Fig. 1) were obtained through the N.C. State Climate Office. All wind variables in this study are described as the direction from which the wind was blowing. Daily averages of wind speed and direction were separated into east–west (u) and north–south (v) components. Thus, the u and v variables represented the magnitude of the wind from each of the orientations. Because recruitment to estuarine habitats may result from the stochastic likelihood that an offshore pool of post-larval crabs coincides with favorable winds, it is possible that the number of days with winds from a particular direction might better represent the influence of wind characteristics on recruitment than the average wind vectors over a period of time. To incorporate information on both wind vectors and number of days of a particular wind direction, these two variables were combined into a single independent variable. It is also likely that the speed of winds, irrespective of direction, could drive recruitment; therefore, we examined wind speed as a separate wind variable. Lastly, the number of tropical cyclones during a time period could impact recruitment levels to different regions. Tropical cyclones were defined as tropical storms or hurricanes that passed within 500 km of the North Carolina CAPES, because tropical cyclones within this distance can influence water levels within the system (L. Xie, Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695, personal communication; L. Etherington, personal observation). We examined the relationship between blue crab recruitment and eight wind variables: (1) u component (east–west); (2) v component (north–south); (3) percentage of days with winds from the east (days with an average east component, rather than west component); (4) percentage of days with winds from the north (rather than south); (5) u component and percentage of days from the east; (6) v component and percentage of days from the north; (7) wind speed; and (8) number of tropical cyclones.

Statistical analyses

The relationship between juvenile blue crab recruitment and wind variables was analyzed using multiple regression. Wind variables included in the model were examined for potential collinearity and were removed from the model when strong collinearity was detected. Plots of variances and predicted values versus residuals were examined to ensure that assumptions of normality and homogeneous variances were met. Outliers were detected using Cook's D statistic and were removed when necessary. The simplest model that explained the most variation in juvenile abundance was determined using Akaike's information criteria, Mallows' C_P statistic, and the adjusted R^2 values (Rawlings et al. 1998). The best fitting models were determined separately for J1–J2 and J3–J5 stages.

For J1–J2 crabs, wind variables were determined from 1 to 21 days before the juvenile sampling period. According to laboratory growth data (Millikin and Williams 1980), J1–J2 blue crabs are about 0–16 days since settlement (Etherington and Eggleston 2000), plus it takes ~5 days for post-larvae to metamorphose to juveniles in the presence of estuarine water (Wolcott and De Vries 1994). Thus, winds 0–21 days before juvenile sampling likely influenced post-larval delivery (primary dispersal) and settlement of individuals that would be sampled later as J1–J2 crabs. For J3–J5 stages, wind variables were determined from 1 to 25 days before the juvenile sampling period (i.e., all days in between the present juvenile sampling and the sampling 1 month prior). Winds during this time period would influence primarily post-settlement dispersal of juveniles (secondary dispersal), which would have settled before this time period, in addition to the delivery and settlement of post-larvae (primary dispersal), which would be later sampled as younger juveniles (J3) (J3–J5 blue crabs are about 14–46 days since settlement; Millikin and Williams 1980; Etherington and Eggleston 2000).

Initially, we examined the relationship between juvenile recruitment and the eight wind variables across all sites. This analysis resulted in a poor fit for both J1–J2 and J3–J5 recruits ($R^2 < 0.10$). Next, we determined the relationship between the various wind variables and juvenile recruitment separately for the inlet versus sound regions. For the inlet region, there was an overall lack of fit between wind characteristics and juvenile recruitment for both size classes (J1–J2, $R^2 = 0.05$; J3–J5, $R^2 = 0.03$). Therefore, we examined the inlet region on a finer spatial scale by analyzing the northern and southern inlets separately because of the difference in geographic orientation between these two coastlines (Oregon inlet, northeastward-facing, versus Hatteras, Ocracoke, and Drum Inlets, which are southeastward-facing; Fig. 1) and potential differences in the interaction of winds with the barrier island topography.

For the sound region, we removed Cedar Island and Oriental (Fig. 1) from our analyses because of consistently low levels of recruitment to these sites (see Results). The aggregation of all sites within the sound region led to a somewhat weak statistical fit between wind variables and juvenile recruitment (J1–J2, $R^2 = 0.15$; J3–J5, $R^2 = 0.15$). Because we were unsure of the specific spatial pathways of post-larval and juvenile transport from a specific inlet to a specific location within the sound region, we were unclear on how to group sites together for statistical analyses. Therefore, we assessed spatial coherence in J1–J2 and J3–J5 densities over time and sites within the sound using Pearson's correlation coefficients. For J1–J2 crabs, there was no clear separation of sites within the sound region, as many of the sites were correlated with one another (Table 1*a*). Thus, we examined the relationship between the density of J1–J2 crabs and wind variables with Engelhard and Swanquarter grouped together (based on relatively close proximity, similar distance from inlet sources of post-larvae, and geographic orientation (Fig. 1)), as well as separate analyses for Manns Harbor and Point Harbor (Fig. 1). For J3–J5 crabs, the correlation analyses indicated that temporal variation in the density of J3–J5 crabs was correlated between Engelhard and Swanquarter; however, density of J3–J5 crabs at Manns Harbor and Point Harbor was not correlated with any other sound sites (Table 1*b*). Thus, similar to our spatial analysis of J1–J2 crabs, we examined the relationship between wind variables and density of J3–J5 crabs at both Manns Harbor and Point Harbor independent of the other sites within the sound region, whereas Engelhard and Swanquarter were analyzed jointly.

Table 1. Spatial coherence of juvenile blue crab recruitment in the sound region as assessed with Pearson's correlation tests.

	PTH	MNH	ENG	SWQ
(*a*) J1–J2 crabs				
PTH	***	0.47	0.84	0.83
		(0.17)	(0.003)	(0.003)
MNH		***	0.13	0.60
			(0.68)	(0.04)
ENG			***	0.47
				(0.12)
SWQ				***
(*b*) J3–J5 crabs				
PTH	***	0.06	0.39	0.56
		(0.86)	(0.27)	(0.09)
MNH		***	0.05	–0.16
			(0.87)	(0.62)
ENG			***	0.80
				(0.002)
SWQ				***

Note: The top value is the Pearson's correlation coefficient and the bottom value in parentheses is the *p* value for the correlation between sites. The sample size ranged from 10 to12. PTH, Point Harbor; MNH, Manns Harbor; ENG, Engelhard; SWQ, Swanquarter.

Post-settlement planktonic dispersal

To determine the role of post-settlement planktonic dispersal in influencing large-scale juvenile blue crab distribution and abundance patterns, we examined site-specific cohorts over time to determine rates of juvenile loss or gain (see below). Laboratory growth data (Millikin and Williams 1980) were used to determine the time-since-settlement of different-sized juveniles, which, in turn, enabled us to define specific cohorts of juvenile blue crabs. Variable growth rates between field and laboratory conditions could alter our estimates of time-since-settlement. Nevertheless, our definition of a cohort is based on the only known data of juvenile blue crab growth and therefore represents the best estimate of a cohort. We examined the density of J1–J2 crabs of 1 month at a particular site and compared this with J5 density for the following month at the same site. As a result, we were able to follow two cohorts per year: (1) August J1–J2 – September J5; and (2) September J1–J2 – October J5 (see Etherington and Eggleston (2000) for further details). We would expect that the number of juveniles in a cohort would decrease over time as a result of mortality and emigration. In instances in which a cohort increased over time (i.e., density of J5 crabs at month $t + 1 >$ density of J1–J2 crabs at month t), we concluded that the cohort had been supplemented by planktonic immigrants. To distinguish an increase in the cohort size over time resulting from post-settlement planktonic dispersal versus an increase resulting from natural variability, we categorized a cohort as increasing only where the error bar of J1–J2 density did not overlap with the error bar of J5 density. It is unlikely that juvenile blue crabs moved from the inlet region to the sound region by walking because of (*i*) the potentially high predation rates of juveniles in unstructured bottom (Pile et al. 1996) and (*ii*) the speed necessary for juvenile crabs to move this distance (to move from the inlet to the sound region by walking, juveniles would have to travel at average speeds between 0.5 and 1.2 km·day^{-1}, speeds far greater than those documented for adult blue crabs (0.25 km·day^{-1}; Shirley and Wolcott 1991)). It also seems unlikely that juveniles are walking to locations within the sound region from nearby habitats, because benthic habitats within this region are very patchy (L. Etherington, personal observation); thus, juveniles would have to traverse large expanses of unstructured habitats where predation is expected to be high (Pile et al. 1996). We examined eight cohorts over the 4-year period (two per year) for juvenile patterns indicative of post-settlement planktonic dispersal. We were also interested in the potential physical forcing mechanisms that caused long-distance planktonic dispersal. To determine if post-settlement planktonic dispersal of juveniles occurred primarily during strong storm events (Etherington and Eggleston 2000), we examined the relationship between the number of tropical cyclones that occurred between the sampling periods for a cohort (cohort 1, August → September; cohort 2, September → October) and the percentage of sites within the sound region that demonstrated abundance patterns representative of post-settlement planktonic dispersal. Percentage rather than number of sites was used as the response variable, because during two time periods (1998, cohort 1; 1999, cohort 2), there were only three sites within the sound that were sampled (versus the other time periods when four sites were sampled).

Results

Environmental conditions

During 1996–1999, the general directional wind patterns at Cape Hatteras shifted during the blue crab recruitment season from an average southwest direction in August to a northeast direction in October (Figs. 2 and 3). There was a large amount of variability in the magnitude as well as direction of the winds during each 3-month blue crab recruitment period (Fig. 2). The 4-year study period contained a relatively high frequency of tropical cyclones, ranging from 2 to 4 per year (Fig. 2). During 1996–1999, tropical cyclones occurred in all months (August–October), with the number of tropical cyclones in a given month ranging from 0 to 2 (Fig. 2). Thus, there was considerable temporal variation in wind forcing with which to examine the response of blue crab recruitment.

Spatial and temporal variation in crab abundance patterns

For the inlet region, the mean density of all stages of early juvenile blue crabs was higher at Oregon and Drum inlets than at Hatteras and Ocracoke inlets (Fig. 4). For the sound region, mean density of J1–J2 crabs was highest at Manns Harbor, followed by Engelhard and Point Harbor, with lowest mean densities at sites in the southern portion of Pamlico Sound (Figs. 4 and 1). For J3–J5 crabs in the sound region, highest densities occurred at Manns Harbor and Engelhard, followed by Point Harbor and the southern sound sites. There was considerable variation in the density of early juvenile blue crabs across years and across months within a year (Fig. 5).

J1–J2 crabs

The density of J1–J2 blue crabs varied significantly according to region, month, and year; however a significant three-way interaction effect of region × month × year (Fig. 5*a*; repeated-measures ANOVA; $F = 4.03$, df = 6,48, $p = 0.002$) prevented clean interpretation of the main effects. In 6 of 12 months sampled, the density of J1–J2 crabs was significantly higher at the inlet region than the sound (Table 2*a*). The density of J1–J2 crabs was never significantly greater in the sound than in the inlets (Table 2*a*). Within the inlet region, September and October contained the highest densities of J1–J2 crabs during the 4-year study (Table 2*b*), whereas within the sound region, there was no particular month that contained significantly higher J1–J2 crab density than the other two months (Table 2*b*). Although annual variation in densities of J1–J2 crabs differed by region and month, 1996 had the highest densities in four of the six month × region combinations (Table 2*c*).

J3–J5 crabs

Densities of J3–J5 blue crabs varied significantly according to year and month; however, a significant year × month interaction effect (Fig. 5*b*; repeated-measures ANOVA; $F = 4.35$, df = 6,48, $p = 0.001$) prevented contrasts across the main effects. The highest density of J3–J5 crabs was in September or October of each year, similar to the pattern for J1–J2 crabs (Table 2 versus Table 3). In 1996, the density of J3–J5 in September and October was significantly higher than the density of J3–J5 in August, whereas in 1998, J3–J5 densities in September were significantly greater than in August and October. In 1997 and 1999 (years with low J3–J5 densities), there was no difference in the density of J3–J5 crabs between months (Table 3). Although there were higher densities of J3–J5 crabs in the sound than the inlet region (Fig. 5*b*), the trend was not significant (Fig. 5*b*; repeated-measures ANOVA; $F = 0.47$, df = 1,8, $p = 0.51$).

Relationship between blue crab recruitment and wind components

In general, the amount of variation in densities of juvenile blue crabs explained by wind forcing, as well as the specific wind variables that showed a positive relationship with juvenile density, varied according to juvenile size class as well as region (Table 4). When examining all sites together, there was a positive relationship between both J1–J2 and J3–J5 crabs and winds; however, winds explained very little of the temporal variation in juvenile density (Table 4). With finer spatial resolution, there was a much stronger relationship between juvenile blue crab density and wind forcing at several locations; however, at other locations, there was a lack of relationship.

At Oregon Inlet, there was a relatively strong relationship between the density of J1–J2 crabs and the strength and number of days of north winds; however, there was a lack of relationship between the density of J3–J5 crabs at Oregon Inlet and wind forcing (Table 4). In contrast to Oregon Inlet, there was no significant relationship between the density of juvenile blue crabs at the southern inlets (Hatteras Inlet, Ocracoke Inlet, Drum Inlet) and wind variables (Table 4). The relationship between the density of juvenile blue crabs and wind variables within the sound region was similar between size classes, but varied between sites within the region. Although juvenile abundance was significantly associated with wind forcing at Engelhard and Swanquarter (Table 4), it was most strongly related to wind forcing at Point Harbor. In contrast, at Manns Harbor, the densities of J1–J2 and J3–J5 crabs were not associated with wind variables (Table 4).

Influence of tropical cyclones on recruitment

We predicted that the spatial distribution of recruitment within the CAPES would increase during the passage of tropical cyclones because of increased primary and secondary dispersal to the sound region. Within the sound region, there did appear to be a positive relationship between the density of J1–J2 crabs and the number of tropical cyclones during September and October of 1996; however, outside of these two periods, densities of J1–J2 crabs in the sound region were extremely low, even during time periods influenced by tropical cyclones. The exception was Manns Harbor, where densities of J1–J2 crabs were moderate to high during most periods. The only site that showed a relationship between J1–J2 density and the number of tropical cyclones was Point Harbor (Table 4). This site is in the uppermost reaches of the CAPES; therefore, strong forcing events may be crucial in dispersal of post-larvae to this area. There was not a strong relationship between the density of J3–J5 crabs and the frequency of tropical cyclones (see below; although one multiple regression model did include the number of tropical cyclones as an explanatory variable; Table 4), suggesting a lack of relationship between secondary dispersal and the number of tropical cyclones. Overall, early juvenile crab abundance in the sound region is not driven solely by the presence or absence of tropical cyclones.

Post-settlement planktonic dispersal

Overall, post-settlement planktonic dispersal appeared to be an important component in juvenile blue crab population dynamics within North Carolina. In seven of the eight cohorts examined, we found evidence of post-settlement planktonic dispersal within at least one of the sound sites as indicated by increased density of crabs within a given cohort at a specific site (Fig. 6). Post-settlement planktonic juvenile

Fig. 2. Alongshore and cross-shelf components of wind velocity as measured at Cape Hatteras National Weather Service Office, N.C., from 1 July to 31 October (days of year 182 to 304) during the years of (*a*) 1996, (*b*) 1997, (*c*) 1998, and (*d*) 1999. The upper graph in each panel represents cross-shelf wind components and the bottom graph represents alongshore wind components. For cross-shelf winds, positive values are easterly winds and negative values are westerly winds. For alongshore winds, positive values are northerly winds and negative values are southerly winds. The direction is the direction from which the wind was blowing. The time periods of juvenile sampling are marked with asterisks, with one sampling period following the new moon in August, September, and October of each year. Tropical cyclones are marked with a letter: 1996, E = Hurricane *Edouard*, F = Hurricane *Fran*, H = Hurricane *Hortense*, J = Tropical storm *Josephine*; 1997, C = Tropical storm *Claudette*, D = Tropical storm *Danny*; 1998, B = Hurricane *Bonnie*, D = Hurricane *Danielle*; 1999, D = Hurricane *Dennis*, F = Hurricane *Floyd*. Wind data is missing from two time periods in 1999 because of the evacuation of the weather service office.

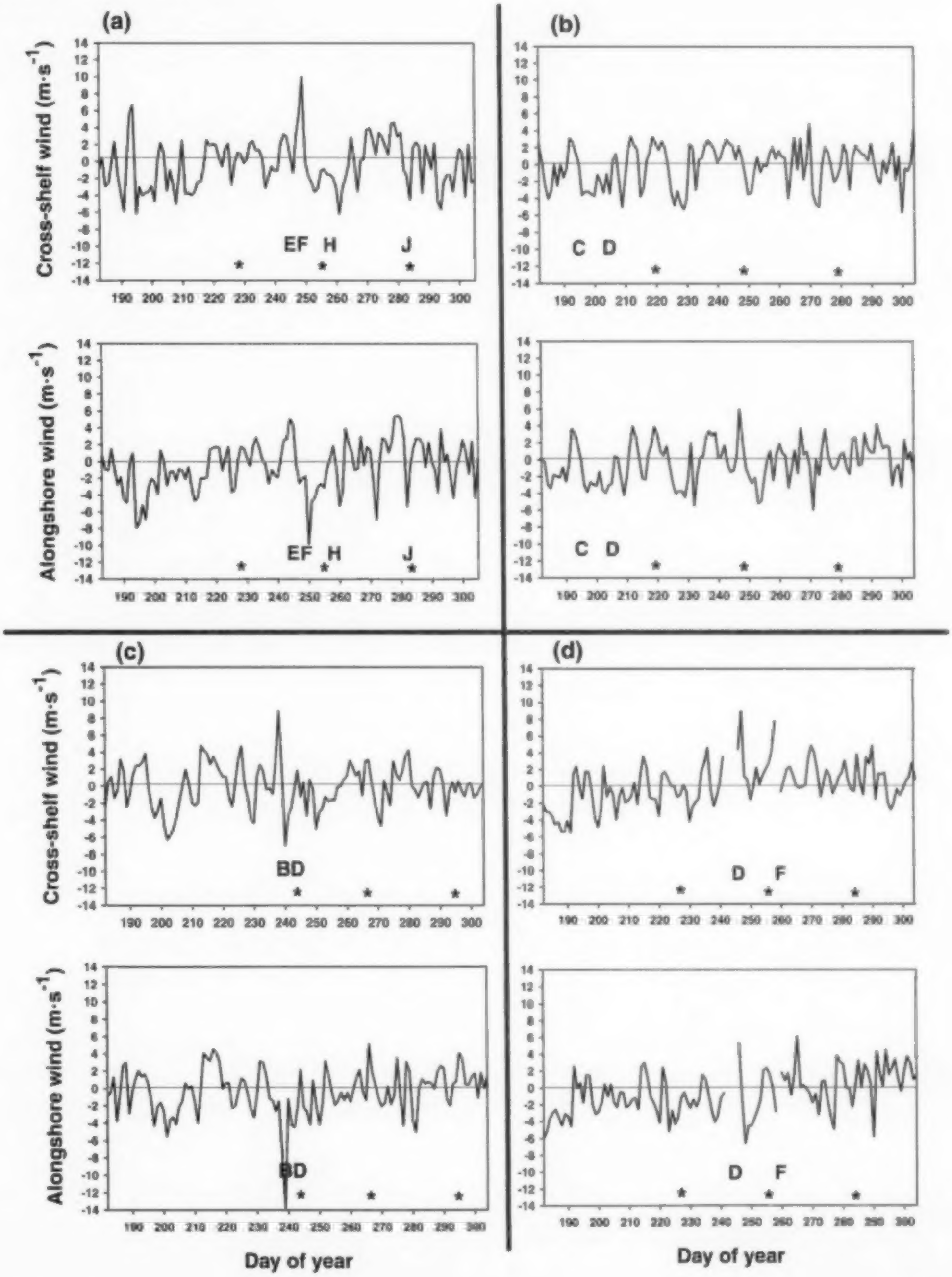
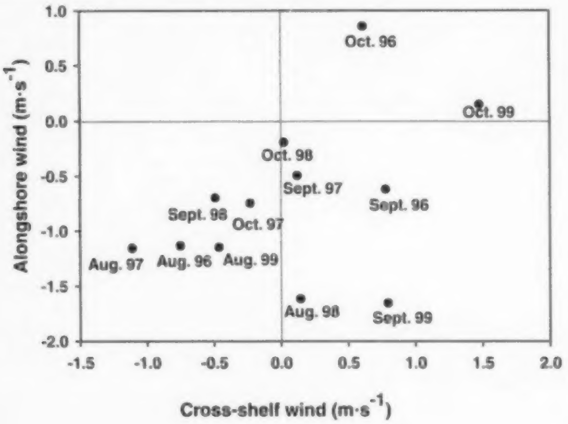


Fig. 3. Average alongshore and cross-shelf components of wind velocity as measured at Cape Hatteras National Weather Service Office, N.C. Wind characteristics were averaged over 25 days before juvenile crab sampling for August, September, and October of the years 1996–1999 (dates represented by two-digit years in the figure). For alongshore winds, positive values are northerly winds and negative values are southerly winds. For cross-shelf winds, positive values are easterly winds and negative values are westerly winds. The direction is the direction from which the wind was blowing. For example, average wind characteristics during August 1996, 1997, and 1999 were from the southwest, whereas winds during September 1996 and 1999 were strong from the southeast, and October 1996 and 1999 were characterized by northeasterly winds.



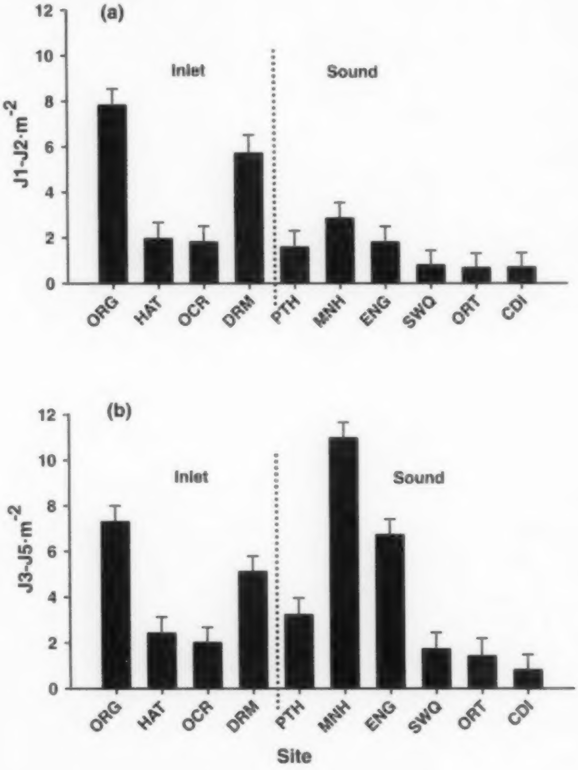
dispersal was detected only at sites within the sound region (except for one case (Cohort 1 of 1999 at Oregon Inlet); Fig. 6). Juvenile abundance patterns indicative of post-settlement dispersal were evident primarily at Engelhard (six of eight cohorts) and Manns Harbor (four of eight cohorts) but were also detected at Swanquarter (four of seven cohorts) and Point Harbor (three of six cohorts) (Fig. 6). The relative increase in cohorts over time was highest at Manns Harbor and Engelhard, suggesting that the magnitude of juvenile dispersal was highest to these sites (Fig. 6).

Contrary to our original hypothesis, there was not a relationship between the percentage of sites within the sound region that showed evidence of post-settlement planktonic dispersal and the number of tropical cyclones (Fig. 7). For example, 57% of the cohorts demonstrating patterns representative of secondary dispersal occurred during periods without tropical cyclones (Fig. 7). These results suggest that post-settlement planktonic dispersal was a consistent process that occurred during a variety of physical conditions, not just during tropical cyclones.

Discussion

We demonstrated that juvenile blue crab distribution and abundance patterns reflect the interaction between primary dispersal of post-larvae and secondary dispersal of early benthic juveniles determined by a suite of wind events that act in a spatially explicit manner. Primary dispersal of post-larval crabs led to spatial clumping within the estuary, with highest densities at relatively seaward locations, particularly Oregon and Drum inlets. Secondary dispersal of post-settlement juveniles occurred soon after benthic settlement (less than 1 month) and increased the distribution of recruits throughout the estuary, potentially broadening the nursery capacity of the system.

Fig. 4. Spatial patterns of (*a*) J1–J2 crabs·m^{-2} and (*b*) J3–J5 crabs·m^{-2} according to site, averaged over all months and years. The vertical dotted line represents the division of the inlet region from the sound region. See Fig. 1 for site name abbreviations. The sites are arranged from north to south, reading from left to right, within each of the regions. Means (+ standard error) represent back-transformed values from means of log-transformed data.



The results from the present study led us to modify our original conceptual model of blue crab recruitment dynamics within the CAPES, whereby under a variety of weather conditions, most post-larvae settle within seagrass beds in the inlet region (donor habitats), with subsequent planktonic dispersal of juveniles to the sound region (receiver habitats). The particular wind events that facilitate primary or secondary dispersal to a particular habitat within the CAPES are highly dependent on the location of habitats within the estuarine system. The overall estuarine distribution of crabs is influenced by a combination of physical forcing processes such as seasonal wind events, the timing and magnitude of tropical cyclones within the recruitment season, and possibly El Niño conditions (predominantly weak offshore winds). Thus, the overall nursery value of different habitats is highly dependent on the dispersal potential (primary and secondary

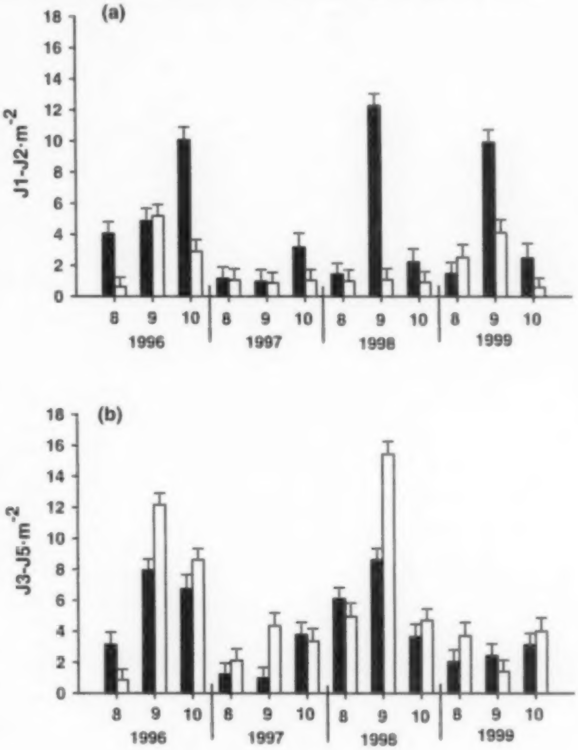


Fig. 5. Juvenile blue crab (*Callinectes sapidus*) recruitment as a function of month (number under bars) and year for (*a*) J1–J2 crabs·m^{-2} and (*b*) J3–J5 crabs·m^{-2} for inlet (solid bars) and sound (open bars) regions. Means (+ standard error) represent back-transformed values from means of log-transformed data.

dispersal) to and from these areas, which is largely a function of the relative position of habitats within the estuarine landscape.

Spatial and temporal variation in crab abundance patterns

The results of this study provide a mechanistic understanding of spatial recruitment patterns that complements observational and simulation studies. For example, Bell et al. (1988) also found that particular locations of seagrass beds within the estuary contained higher settlement of many species of fish and decapod crustaceans than at other locations because of their relative proximity to spawning areas. Similarly, Heck and Thoman (1984) detected higher densities of blue crabs within seagrass habitats in the lower versus the upper Chesapeake Bay because of juvenile recruitment at locations closer to oceanic environments where they were spawned. A simulation modeling study of blue crab post-larval settlement within the Chesapeake Bay illustrated that the "value" of a particular seagrass habitat can depend on its location within the estuarine landscape because of the likelihood of post-larval settlement (Stockhausen and Lipcius 2003). These studies illustrate how the relative position of habitats within the landscape can influence their overall value as nursery habitats and emphasize the importance of hydrodynamics in marine systems in influencing individual responses to the spatial pattern of landscape mosaics (Robbins and Bell 1994).

The size- and region-specific patterns of intra-annual juvenile recruitment to the CAPES could result from the interaction between temporal variation in the oceanic pool of larvae with meteorological and physical–oceanographic conditions along the continental shelf of North Carolina. For example, J1–J2 crab density within the inlet region and J3–J5 densities across the CAPES were greatest in September and October, months that have favorable winds to deliver post-larvae into Oregon Inlet (see below). August and September represent a transition from spring–summer conditions, which typically exhibit variable winds from the south, to fall–winter conditions beginning in October, which typically involve northerly winds (Miller et al. 1982; Epifanio and Garvine 2001). In addition to more favorable winds in September and October, the occurrence of post-larval crabs in continental shelf waters may also be greater later in the fall (Epifanio et al. 1984) because of greater frequency of spawning in early fall than late summer. September and October also happen to be months in which the North Carolina coast experiences a large number of tropical cyclones, adding an additional mechanism to facilitate transport of post-larval crabs into the estuarine system. Thus, the intra-annual variation in juvenile blue crab abundance may reflect the interaction between the available larval pool and favorable winds.

The density of juvenile blue crabs also showed considerable variation between years. For example, the densities of J1–J2 crabs in 1996 and 1999 were relatively large, most likely because of the interaction of favorable winds and tropical cyclones. An unusually large peak of J1–J2 crabs is apparent in September 1998 that cannot be attributed to tropical cyclone delivery of post-larvae. Instead, the high abundance of J1–J2 in September of 1998 may represent a large recruitment pulse owing to a large spawning stock size that year, as detected in a fishery-independent trawl survey (1998 was one of the top two years in spawning stock biomass in the last 14 years, and there is a significant spawning stock–recruit relationship for the blue crab in North Carolina; Eggleston 1998). It is noteworthy that 1997 exhibited strong El Niño conditions, whereas the other years in this study were non-El Niño years (based on values of the standardized Southern Oscillation Index (SOI) found at www.cpc.ncep.noaa.gov/data/indices/). It is possible that the weather conditions associated with El Niño events (predominantly weak offshore winds) could influence overall juvenile recruitment and could have contributed to the particularly low densities of J1–J2 crabs in 1997. Overall, variation in juvenile blue crab abundance between years could be a reflection of meso- and large-scale meteorological processes (e.g., tropical cyclones and El Niño), as well as the size of the spawning stock.

Relationship between blue crab recruitment and wind components

When examined on an estuarine-wide scale, temporal variation in juvenile recruitment could not be explained by wind variables; however, when examined by site or region, wind characteristics were a fairly good predictor of juvenile density. For example, the relatively strong relationship between

Table 2. Ryan's *Q* test of the mean number of J1–J2-stage (log(x + 1)-transformed) blue crab instars per 1.67 m^2 for the region × month × year interaction effect.

(*a*) Month and year × region.

Month–year	Region	
August–1996	Sound	Inlet
September–1996	Inlet	Sound
October–1996	Sound	Inlet
August–1997	Sound	Inlet
September–1997	Sound	Inlet
October–1997	Sound	Inlet
August–1998	Sound	Inlet
September–1998	Sound	Inlet
October–1998	Sound	Inlet
August–1999	Inlet	Sound
September–1999	Sound	Inlet
October–1999	Sound	Inlet

(*b*) Region and year × month.

Region–year	Month		
Inlet–1996	8	9	10
Inlet–1997	9	8	10
Inlet–1998	8	10	9
Inlet–1999	8	10	9
Sound–1996	8	10	9
Sound–1997	9	10	8
Sound–1998	10	8	9
Sound–1999	10	8	9

(*c*) Region and month × year.

Region–month	Year			
Inlet–August	1997	1998	1999	1996
Inlet–September	1997	1996	1999	1998
Inlet–October	1998	1999	1997	1996
Sound–August	1996	1998	1997	1999
Sound–September	1997	1998	1999	1996
Sound–October	1999	1998	1997	1996

Note: Treatment levels that are not significantly different at $\alpha = 0.05$ share an underline. Treatment levels are arranged in increasing order of density.

Table 3. Ryan's *Q* test of the mean number of J3–J5 (log(x + 1)-transformed) blue crabs per 1.67 m^2 for the month × year interaction effect.

Year	Month		
1996	8	10	9
1997	8	9	10
1998	10	8	9
1999	9	8	10

Note: Treatment levels that are not significantly different at $\alpha = 0.05$ share an underline. Treatment levels are arranged in increasing order of density.

densities of J1–J2 and J3–J5 crabs and northerly winds at Oregon Inlet was consistent with the relationship between blue crab post-larval settlement to Oregon Inlet and northerly wind speed (D. Eggleston, unpublished data). Northerly winds, which are often associated with the passage of low-pressure systems in the early fall, cause onshore Eckman flow that facilitates transport of blue crab post-larvae into estuaries within the Mid-Atlantic Bight (Epifanio and Garvine 2001), as has been observed in several field studies along the western Atlantic (Goodrich et al. 1989; Little and Epifanio 1991; Jones and Epifanio 1995). On the continental shelf, blue crab post-larvae remain in the surface waters (Epifanio 1995); thus, post-larvae would be transported in the 5- to 15-m-thick surface layer during fall conditions (Miller et al. 1982). Within the CAPES, surface flow tends

Table 4. Best-fit multiple regression models describing the relationship between wind variables and the density of J1–J2 and J3–J5 blue crabs within each study region.

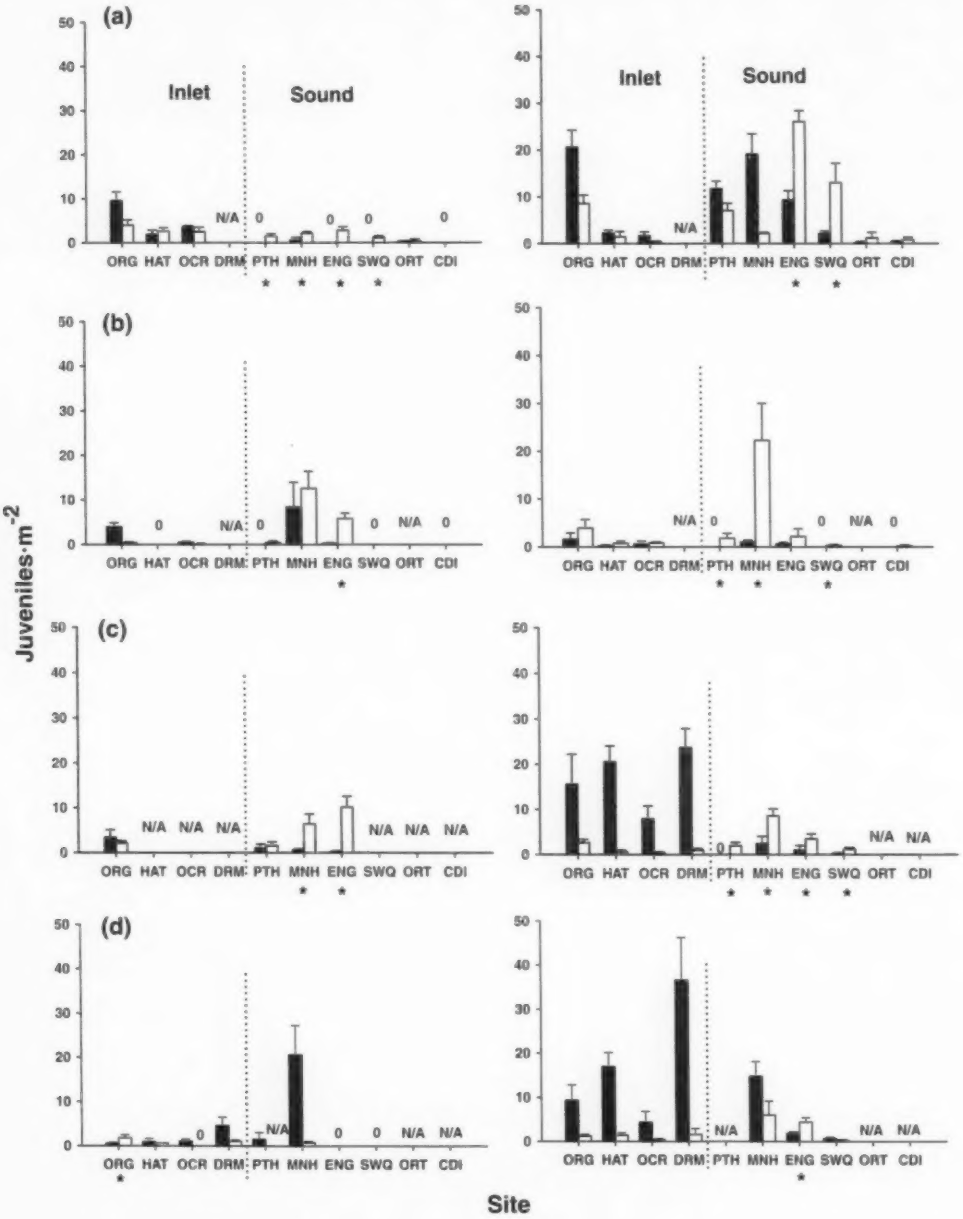
	All sites ($n = 88$)	Oregon inlet ($n = 12$)	Southern inlets ($n = 30$)	PTH ($n = 10$)	MNH ($n = 12$)	ENG and SWQ ($n = 24$)
J1–J2	$R^2 = 0.07$ $p = 0.01$ Strength of east winds ($p = 0.01$)	$R^2 = 0.71$ $p = 0.0006$ Strength and % days of north winds ($p = 0.0006$)	$R^2 = 0.10$ $p = 0.21$ % days of south winds ($p = 0.12$) % days of east winds ($p = 0.14$)	$R^2 = 0.75$ $p = 0.008$ Strength of east winds ($p = 0.02$) No. of tr. cyclones ($p = 0.03$)	$R^2 = 0.19$ $p = 0.16$ Strength and % days of north winds ($p = 0.16$)	$R^2 = 0.29$ $p = 0.03$ Wind speed ($p = 0.02$) Strength of north winds ($p = 0.04$)
J3–J5	$R^2 = 0.06$ $p = 0.02$ Strength of north winds ($p = 0.02$)	$R^2 = 0.03$ $p = 0.62$ Strength of north winds ($p = 0.62$)	$R^2 = 0.08$ $p = 0.13$ % days of west winds ($p = 0.13$)	$R^2 = 0.64$ $p = 0.006$ Strength of east winds ($p = 0.006$)	$R^2 = 0.23$ $p = 0.11$ "–" wind speed ($p = 0.11$)	$R^2 = 0.35$ $p = 0.01$ Strength of north winds ($p = 0.01$) No. of tropical cyclones ($p = 0.10$)

Note: Southern inlets: Hatteras, Ocracoke, and Drum. PTH, Point Harbor; MNH, Manns Harbor; ENG, Engelhard; SWQ, Swanquarter. Sample sizes for the models are given below the region title. p values are given for the whole model, as well as for each of the independent variables included in the model (p values for each of the variables included in model are in parentheses). All parameter estimates are positive, except where noted as "–".

to be directed with the wind, with water current speeds approximately 0.01 of the wind velocity (Pietrafesa et al. 1986). Because of the shallow depth of the estuarine system and the influence of wind mixing, there is virtually no vertical stratification in the CAPES (Pietrafesa et al. 1986). Thus, the transport mechanism for primary and secondary dispersal, as well as cues initiating secondary juvenile dispersal, should be integrated over all depths. Computer simulations of surface and bottom currents demonstrate that north and northeasterly winds produce a strong exchange of water between the coastal ocean and the estuary; however, inwelling occurs primarily through Oregon Inlet, with outwelling at Hatteras and Ocracoke inlets (Xie and Eggleston 1999). Thus, northerly winds appear to be favorable in transporting post-larvae only through Oregon Inlet and may impede the transport of post-larvae through the southern inlets because of differences in the orientation of the coastlines. Transport of post-larvae into the southern inlets may be driven more by tidal forcing, owing to the lack of a southern-driven buoyancy current along this part of the coastline (Epifanio and Garvine 2001), which would have the potential to dampen tidal forcing, if present. Our results agree with a study of larval fish abundance in North Carolina that also detected differences between Oregon and Ocracoke inlets, with most fish species exhibiting different times of occurrence and peak abundance between Oregon Inlet and Ocracoke Inlet (Hettler and Barker 1993). Thus, temporal variation in wind conditions could create spatial variation in juvenile recruitment to inlet areas north and south of Cape Hatteras.

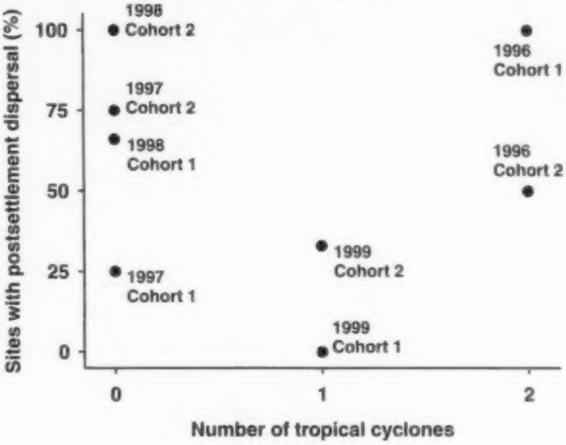
Although the wind characteristics that influenced the density of juvenile crabs within the sound region varied according to areas within the region, there were fairly consistent results between J1–J2 and J3–J5 size classes. At Point Harbor, the densities of J1–J2 and J3–J5 crabs were strongly dependent on the strength of east winds. Easterly winds relax the southward surface flow from Croatan Sound to Pamlico Sound that is present during most other wind events (Xie and Eggleston 1999), allowing primary post-larval dispersal and secondary juvenile dispersal northward into Albemarle Sound. There was also a relationship between J1–J2 stages and tropical cyclones, suggesting that primary dispersal of post-larvae into the Point Harbor area can occur during strong wind events. Recruitment variation of both J1–J2 and J3– J5 crabs at Engelhard and Swanquarter could also be explained by particular wind events, specifically the magnitude of northerly winds and strong forcing events (J1–J2, wind speed; J3–J5, tropical cyclones), which could be responsible for facilitating primary dispersal of post-larvae or secondary dispersal of post-settlement juveniles into these areas. These results match our findings of high post-larval settlement to Engelhard during strong forcing events (D. Eggleston, unpublished data). In contrast to the other sites within the sound region, the density of juvenile crabs within Manns Harbor could not be explained by particular wind characteristics. These results suggest that post-larval and juvenile dispersal to this area could occur during a variety of different wind events or, instead, that other forcing mechanisms, such as tidal flow (which may persist this far into the estuary), could play a role in dispersing crabs to the Manns Harbor area. The results from this study illustrate that the relation-

Fig. 6. Analysis of site-specific cohort abundance over a 1-month period for two separate cohorts for the years (*a*) 1996, (*b*) 1997, (*c*) 1998, and (*d*) 1999. Cohort 1 (left panels) is defined by J1–J2 crabs in August and J5 stage crabs in September. Cohort 2 (right panels) is defined by J1–J2 crabs in September and J5 crabs in October. See Fig. 1 for site name abbreviations. Values are means + standard error. N/A denotes sites that were not sampled in that time period. Post-settlement dispersal within a cohort is evident where the abundance of J5 (open bars) is greater than J1–J2 (solid bars) at a given site and where the error bar of J1–J2 density does not overlap with the error bar of J5 density. Juvenile patterns indicative of post-settlement dispersal are marked with an asterisk (*) below the site name. Seven of the eight cohorts exhibited post-settlement dispersal (where at least one site within a cohort exhibited dispersal) to sites within the sound region. Cohort 1 of 1999 was the only cohort that did not exhibit post-settlement dispersal to the sound sites.



ship between recruitment and different wind characteristics can depend on the spatial location within the estuary, emphasizing the need to examine the influence of local topography on physical–biological coupling to understand spatial heterogeneity of dispersal between the oceanic and estuarine environments.

Fig. 7. Relationship between the number of tropical cyclones that occurred between the sampling periods of each cohort (cohort 1, August → September; cohort 2, September → October) and the percentage of sites within the sound region that exhibited evidence of post-settlement planktonic dispersal of juvenile crabs.



Relationship between recruitment and tropical cyclones

The timing of tropical cyclones within an organism's recruitment season may influence the overall impact of strong storm events on dispersal of post-larval and juvenile stages. Strong water forcing by hurricanes occurring early in the blue crab recruitment season (August) may not have much influence on overall recruitment because blue crab post-larvae are not as common in shelf waters during this time period (compared with September and October) (Epifanio et al. 1984). In our 4-year study, the two years that had hurricanes later in the season (September and October) had higher densities of J1–J2 crabs compared with years with tropical cyclones in August. It was also apparent that the cohorts in 1999 generally demonstrated the lowest percentage of sites with post-settlement dispersal, with cohort 1 of 1999 being the only cohort during the 4 years that did not exhibit patterns indicative of post-settlement dispersal at any of the sound sites. It is noteworthy that freshwater floodwaters from three sequential hurricanes (Dennis, Floyd, Irene) in September 1999 displaced three-quarters of the volume of Pamlico Sound (Paerl et al. 2001), which may have disrupted across-sound transport mechanisms. Finer-scale current data and planktonic sampling are needed within the CAPES to understand blue crab dispersal trajectories during tropical cyclones of various magnitudes, directions, and temporal occurrences within the recruitment season.

Post-settlement planktonic dispersal

In this study, secondary dispersal of early post-settlement juveniles modified initial distribution and abundance patterns of J1–J2 blue crabs. It is well known that secondary dispersal occurs in the blue crab (e.g., dispersal away from nursery areas, movement towards lower salinity mating areas, female migration towards oceanic waters to spawn; Van Engel 1958). The unique contribution of the present study is that a large amount of secondary dispersal is occurring very early in the life history of post-settlement crabs and that a substantial amount of it occurs in the plankton. As a result, processes in the water column assume a greater importance, because planktonic dispersal is a mechanism causing high connectivity between initial settlement and adult habitats. Moreover, distribution and abundance patterns established after secondary dispersal of early juvenile crabs match subsequent distribution and abundance patterns of later-stage juveniles (Eggleston 1998). These results suggest that secondary dispersal soon after benthic settlement is a key determinant in blue crab distribution and abundance within the CAPES.

In conclusion, recognition that distribution and abundance patterns of benthic marine organisms can be jointly influenced by primary dispersal to initial settlement sites and large-scale secondary dispersal can aid in our understanding of life stage dependent habitat connectivity, population dynamics, and the scales at which local ecological processes operate (Palmer et al. 1996). For example, secondary dispersal of individuals soon after settlement indicates that initial settlement patterns are not fixed and that there is the potential for high connectivity between spatially separated regions. High connectivity between spatially separated habitats suggests that regions of varying recruitment and habitat quality may be linked as donor and receiver areas. Our results indicate that donor and receiver regions were fairly consistent between years; however, the degree of connectivity appeared to be influenced by large-scale meteorological forcing mechanisms. This study also demonstrated that planktonic secondary dispersal soon after benthic settlement is a key determinant of population distribution and abundance patterns of later stage juveniles, suggesting that local dynamics can be strongly influenced by regional processes. Dispersal can also alter population dynamics by aggregating individuals (primary dispersal) or broadening the distribution of recruits (secondary dispersal). Our results emphasize the need to consider the dispersal potential and the spatial position of habitats within the landscape to determine their value as nursery habitats (Beck et al. 2001). High connectivity between habitats emphasizes the dependence between multiple regions and advocates the need to consider multihabitat management at the scale of the estuary (e.g., Roberts 1997). Thus, studies of multistage dispersal will aid in our understanding of habitat loss, spatial isolation of habitats, and the scales at which conservation efforts should be directed. Physical forcing can determine the relative influence of primary and secondary dispersal, therefore, changing the degree of connectivity between regions, modifying local population dynamics, and altering spatial patterns of habitat use. This study identified how physical processes, which are acting on different spatial and temporal scales (from local events lasting hours or days, to interannual patterns), interact to influence dispersal during multiple stages of an organism's life cycle and the resulting consequences on recruitment.

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Relationships between organic matter composition and methyl mercury content of offshore and carbon-rich littoral sediments in an oligotrophic lake

Martin Kainz, Marc Lucotte, and Christopher C. Parrish

Abstract: Relationships between organic matter (OM) compounds and methyl mercury concentrations ([MeHg]) have been examined in littoral and offshore sediments of Lake Lusignan (Québec). The highest [MeHg] were generally found at the sediment–water interface with exceptionally high concentrations at littoral sites (5.8 ± 1.3 ng·g dry weight^{-1}), which were four times more elevated than at offshore sites (1.6 ± 0.77 ng·g dry weight^{-1}). Source-specific fatty acid (FA) biomarkers identified that littoral sediments contained more than twice as much terrestrial and bacterial OM compounds than offshore sediments, whereas the amount of labile algal OM was three times higher at littoral sites. Results indicate that [MeHg] were higher in the presence of labile OM substrates, and the amount of terrestrial OM compounds could not predict [MeHg]. Correlations between [MeHg] and FA of *Desulfovibrio desulfuricans* (a sulfate-reducing bacterium producing MeHg) could significantly account for 36% of [MeHg] at offshore sites; however, no significant relationships were found at littoral sites. This study illustrates that the microbial dynamics involved in producing and degrading MeHg in lacustrine sediments are complex and cannot be predicted solely by the quantification of FA biomarkers in *D. desulfuricans* or by biomarkers in the OM itself.

Résumé : Nous avons examiné les relations entre la matière organique (MO) et les concentrations du méthylmercure (MeHg) dans les sédiments littoraux et pélagiques du lac Lusignan (Québec). En général, les concentrations du MeHg les plus élevées ont été trouvées à l'interface sédiment–eau dans les zones littorales (5,8 ± 1,3 ng·g poids sec^{-1}). Les concentrations étaient quatre fois plus élevées que celles mesurées dans les zones pélagiques (1,6 ± 0,66 ng·g poids sec^{-1}). Les analyses des acides gras (AG), utilisés comme biomarqueurs des sources de MO, ont permis d'établir qu'il y avait deux fois plus de MO terrigène et bactérienne et trois fois plus de MO labile provenant des algues dans les sédiments littoraux que dans les sédiments pélagiques. Nos résultats montrent que les concentrations en MeHg étaient plus élevées en présence de MO labile et que la quantité de MO terrigène ne pouvait pas prédire les concentrations du MeHg. Les corrélations entre les concentrations du MeHg et des AG de la bactérie *Desulfovibrio desulfuricans*, une bactérie sulfato-réductrice impliquée dans la dynamique du MeHg, pouvaient expliquer 36 % de la présence du MeHg dans les sites pélagiques. Par contre dans les sites littoraux, ces corrélations n'étaient pas significatives. Notre étude démontre que les dynamiques microbiennes impliquées dans la production et la dégradation du MeHg dans les sédiments lacustres sont complexes et la quantification des biomarqueurs des AG trouvées dans *D. desulfuricans* ou les AG de la MO ne peuvent pas prédire les teneurs en MeHg dans les sédiments.

Introduction

Sediments can be a source of mercury (Hg) contamination for lake biota (e.g., Tremblay et al. 1998). Bodaly et al. (1984) associated high Hg concentrations ([Hg]) in fish with bacterial methylation of Hg in flooded soils because flooding of terrestrial material may have facilitated access for bacteria to carbon sources, which subsequently increased microbial activity and bacterial Hg methylation. The presence of methyl mercury concentrations ([MeHg]) in sediments can be influenced by processes including historical MeHg loading (Gagnon et al. 1996), in situ methylation and demethylation (e.g., Pak and Bartha 1998*a*), activity of sulfate-reducing bacteria (e.g., Gilmour et al. 1992), and HgS precipitation by methylating bacteria (Benoit et al. 1999).

It is recognized that organic matter (OM) in sediments serves as an energy-yielding substrate for bacteria involved in the cycling of MeHg (Compeau and Bartha 1985). The

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amount of OM in sediments was also found to be positively correlated with Hg methylation activity (Choi and Bartha 1994). However, detailed information on the biochemical composition of OM, e.g., algal, bacterial, and terrestrial substances of sediments, and its relationship with MeHg is scarce.

Lipids are an important class of natural OM and have been widely used as biomarkers in biogeochemical studies on sediments (e.g., Sun and Wakeham 1994). Fatty acids (FA) are major constituents of lipids, and their molecular composition (Parrish 1999) provides useful information about the origin of OM in sediments. Recently, Desvilettes et al. (1997) have identified a number of polyunsaturated FA (PUFA) as algal biomarkers and odd-branched FA as bacterial biomarkers, and saturated and longer FA chains (≥C24:0) have been detected in OM of terrestrial origin (e.g., Sun and Wakeham 1994). Because FA biomarker compounds retain quantifiable evidence of their respective algal, bacterial, or terrestrial origin, they provide detailed information about the OM composition of sediments.

We examine whether the quality of sedimentary OM composition can predict the presence of MeHg in littoral and offshore sediments of the oligotrophic Lake Lusignan, Quebec. In particular, we test the hypotheses that [MeHg] in sediment profiles are positively correlated with the quantity of bacterial biomarkers found in Hg-methylating bacteria and that the presence of bacterial biomarkers can be used as indicators for MeHg dynamics in sediments. By using FA biomarkers as source indicators, we determine the distribution of algal, bacterial, and recalcitrant terrestrial OM at different sediment layers. By applying this biomarker method, we obtain detailed information on how MeHg is associated with the algal, bacterial, and terrestrial OM composition of sediments.

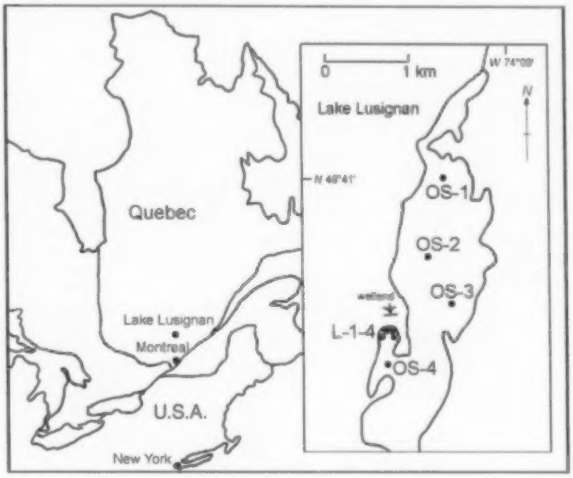
Materials and methods

Study site and sampling

Sampling was conducted in August 1999 at the oligotrophic (3.7 ±1.2 μg chlorophyll *a* (chl *a*)·L^{-1}) Lake Lusignan (Quebec, Canada; 46°41′N, 74°09′W). In the 1950s, this lake was dammed to facilitate the flotation of logs, and the water level has been raised 2 m and maintained since then. Flotation activities stopped in the late 1960s. The average sedimentation rate at the deepest lake station was calculated to be 0.24 cm·year^{-1} (Lucotte et al. 1995). Although no sedimentation data are available for littoral sediments, it is possible that OM deposition at littoral sites exceeds sedimentation rates of profundal locations (Petticrew and Kalff 1992). Based on the profundal sedimentation rate, it is clear that analyzed sediment material was deposited after flooding.

Offshore sites were chosen at the deepest spots of different lake basins. Sediment samples were taken at four offshore sites (OS-1, 4 m; OS-2, 10 m; OS-3, 22 m, the deepest lake station; OS-4, 4 m) and four littoral sites that included macrophyte beds (L-1–L-4, 1 m; Fig. 1). OS-2 and OS-3 were both located in aphotic profundal zones, whereas OS-1 and OS-4 (both free of sediment vegetation) were not aphotic and so represent transitional sites (Wetzel 2001). The epilimnetic water temperature was 18 °C (YSI Model 3800; YSI Inc., Yellow Springs, Ohio) and thermal stratification started at 8 m deep. All cores were collected by divers using polyvinyl chloride (PVC) box cores. The sediment–water interface (SWI; 0 cm) was sampled with a 60-mL plastic syringe. The cores were sectioned at intervals of 0.5 cm for the first 5 cm; thereafter samples were taken at each centimetre. Sediment samples were kept frozen at −20 °C in polypropylene vials until lyophilization. Freeze-dried samples were stored at −20 °C until analysis.

Fig. 1. Lake Lusignan (Quebec, Canada) with littoral (L) and offshore (OS) sediment stations.



Analysis

For total Hg (THg) analysis, all sediment samples were freeze-dried for 3 days before acid digestion. All labware was acid washed in 10% HCl, triple-rinsed with NANOpure® water (Millipore Corp., Billerica, Mass.) and then heated to 300 °C for 8 h. [THg] were determined using atomic fluorescence spectrometry (AFS). The analytical method is described in detail by Pichet et al. (1999). Briefly, 200–500 mg (dry weight, DW) sediment aliquots were transferred to glass tubes and digested in 10 mL of a 10:1 16N HNO_3 – 6N HCl mixture, heated at 121 °C for 6 h, and subsequently diluted with NANOpure® water. THg was then reduced to elemental Hg (Hg^0) vapour by a tin chloride ($SnCl_2$) solution in a reaction vessel, and the Hg^0 was analysed by AFS. Both the accuracy of this method (tested by analysing different standards that yielded mean concentrations comparable with the certified values) and its reproducibility were 4–5% (Pichet et al. 1999). Its detection limit, three times the standard deviation of procedural blanks, was 75 pg of Hg. The accuracy of the method was verified by analysing a National Research Council of Canada standard (BEST-1).

The determination of sedimentary [MeHg] was performed by a two-step analysis technique. Freeze-dried sediment samples (200 mg) were first digested in an acid solution (6N HCl and $CuSO_4$) to release the MeHg content. The liberated MeHg was then taken up by three sequential extractions using 2 mL of toluene to completely capture all MeHg. Those three extractions were transferred into one test tube. The 6-mL extract was then partially evaporated to a final volume of 0.2–0.5 mL. This extraction (50 μL) was injected into a gas-chromatograph (GC) column (coated with 10% free fatty acid phase). MeHg was carried through a 140 °C heated column by a 60 mL·min^{-1} argon flux. Subsequently, MeHg was thermally decomposed to Hg^0 in a 400 °C heated tube filled with quartz wool and eventually analysed by AFS (see Pichet et al. 1999). Accuracy was checked by standard addition measurements, which gave a 90 ± 10% recovery rate. The detection limit (3 standard deviations) was 0.02 ng Hg·g^{-1}.

Levels of total organic carbon (TOC) and nitrogen were measured using a CN Carlo-Erba autoanalyzer (model NA 1500 series 2; CE Instruments, ThermoQuest Italia S.p.A., Rodano (MI), Italy) with a reproducibility of ~1% (RSD). Because of the negligible concentration of carbonates in sediment samples (Courcelles 1998), total carbon represents TOC.

For chl *a* sampling, 1 L of lake water was filtered through a Gelman GF/F filter. The filters were kept frozen until chl *a* was extracted with 90% hot ethanol, followed by spectrophotometer measurements before and after acidification.

Values of the redox potential were taken directly from the sediment cores by a portable Eh meter (ORION 250A™; Thermo Electron Corp., Beverly, Mass.). The Eh-design consists of a silver/silver chloride reference element that forms a conductive bridge between this reference electrode, the sediment samples, and an indicating electrode that has been inserted into the core. Tiny holes were drilled along the box cores and sealed before the recovery of the cores to prevent air passage.

Lipids from ~100 mg of homogenized, freeze-dried sediment samples were extracted in chloroform–methanol. Hexane and BF_3/CH_3OH were added to lipid extracts for fatty acid methyl ester (FAME) formation as described in detail elsewhere (Kainz et al. 2002; Parrish 1999). FAME was analysed using a GC – flame ionization detection (FID) system (Varian 3400; Varian, Inc., Palo Alto, Calif.) equipped with a temperature-programmable injector and an autosampler (Varian 8100) as described by Kainz et al. (2002).

Results

THg, MeHg, and TOC concentrations and redox conditions (Eh)

Profiles of [THg], [MeHg], and [TOC] are presented for littoral (Fig. 2) and offshore (Fig. 3) sediments. [THg] showed rather homogenous downcore profiles at 150 ng·g^{-1} in littoral cores, whereas [THg] in OS-1, -2, and -3 were variable between the SWI and 10-cm depth, which may have been due to perturbation or inconsistent deposition. The highest [THg] were found at the deepest offshore station (OS-3) and the lowest concentrations were detected at OS-4.

[MeHg] generally decreased rapidly from the SWI downcore. At the SWI, [MeHg] were between two and eight times higher at littoral (mean 3.6 times; Table 1) than at offshore sites. Within the first 5 cm, decreases of [MeHg] were higher in offshore than littoral cores (Table 2). The percentage of methylated Hg was higher in littoral than in offshore sediment cores (Fig. 4); however, the relative amount of methylated Hg at the 5-cm depth was lower in offshore than in littoral sediments (8% and 25%, respectively) when compared with the relative amount of methylated Hg at the SWI.

[TOC] ranged from 100 to 250 mg·g DW^{-1} in offshore and from 400 to 500 mg·g DW^{-1} in littoral cores. Although the atomic C/N ratios (14–21 in offshore cores) were significantly different among the offshore cores (paired *t* test, $P < 0.05$), they were distinctly smaller than the atomic C/N ratios in littoral cores (28–39). In each core, this ratio was lower at the SWI than in segments further below.

Offshore sediment cores became anoxic within a few millimetres below the SWI. Redox conditions in littoral cores indicated that beneath oxic surficial sediments there was a less rapid transition to anoxic conditions at about 2 cm.

FAME

Total identified [FAME] ($C_{14:0}$–$C_{24:1}$) of offshore and littoral sediments are reported elsewhere (Kainz 2001). Mean [FAME] from the littoral sites were significantly higher than those from offshore sediments (Table 1).

Saturated fatty acids (SAFA)

In general, [SAFA] steadily increased from the sediment surface downcore. We present myristic (C14:0) and lignoceric (C24:0) acids as indicators for phytoplankton and terrestrial OM, respectively (Sun and Wakeham 1994). Ratios between the two acids (C24:0/C14:0) indicated mean values of 2.2 (±0.2) and 4.5 (±0.3) at the SWI for offshore and littoral sediments, respectively. Lignoceric acid concentrations from littoral sediment sites were on average six times higher than those from offshore sites. Moreover, C24:0/C14:0 ratios were significantly different between offshore and littoral stations and increased with sediment depth (Fig. 5).

Bacterial fatty acids

Bacterial biomarkers, identified as odd-chain, branched-chain (*iso-* and *anteiso*-series) FA, as well as saturated C15:0 and C17:0 FA components, accounted for 10% of total FAME in offshore sediments and 7% in littoral sediments. However, bacterial [FA] were over 2.2-fold higher in upper littoral than in offshore sediments (Table 1). Bacterial markers decreased in all cores from the SWI downcore. The abundance of these indicators at the deepest stations, OS-2 and OS-3, was reduced by 25% at the 5-cm depth, whereas the concentrations of bacterial FA in OS-1 and OS-4 were lowered by 57% and 66%, respectively. Similar trends were present in littoral cores (i.e., 25%, 54%, 33%, and 21% in L-1, -2, -3, and -4, respectively).

Unsaturated fatty acids

Concentrations of total monounsaturated and polyunsaturated FA decreased with sediment depth in both offshore and littoral sediments. Although absolute surficial [PUFA] were three times higher in littoral than in offshore cores (Table 1), no significant difference in PUFA percentages of total FAME could be detected between littoral and offshore profiles (see Kainz 2001).

Statistical analyses

[MeHg], [FAME], [bacterial FA], and algal biomarkers ([PUFA]) decreased more at offshore than at littoral sites between the SWI and 5-cm depth (Table 2); however, because of the high intercore variability, differences between offshore and littoral sites were not statistically significant (paired *t* test, $P > 0.05$). Using analysis of covariance (ANCOVA) to correct for sediment station, concentrations of PUFA, bacterial FA, *iso*-15:0, and *iso*-17:0 in offshore sediment cores

Fig. 2. Profiles of redox potentials (Eh; open circles with solid line), MeHg (solid circles with solid line) and total Hg (THg; solid triangles with solid line) concentrations, total organic carbon concentrations (TOC%; solid circles with broken line), and atomic carbon–nitrogen ratios (C/N; open circles with broken line) in the four littoral sediment cores: (*a*) L-1; (*b*) L-2; (*c*) L-3; and (*d*) L-4.

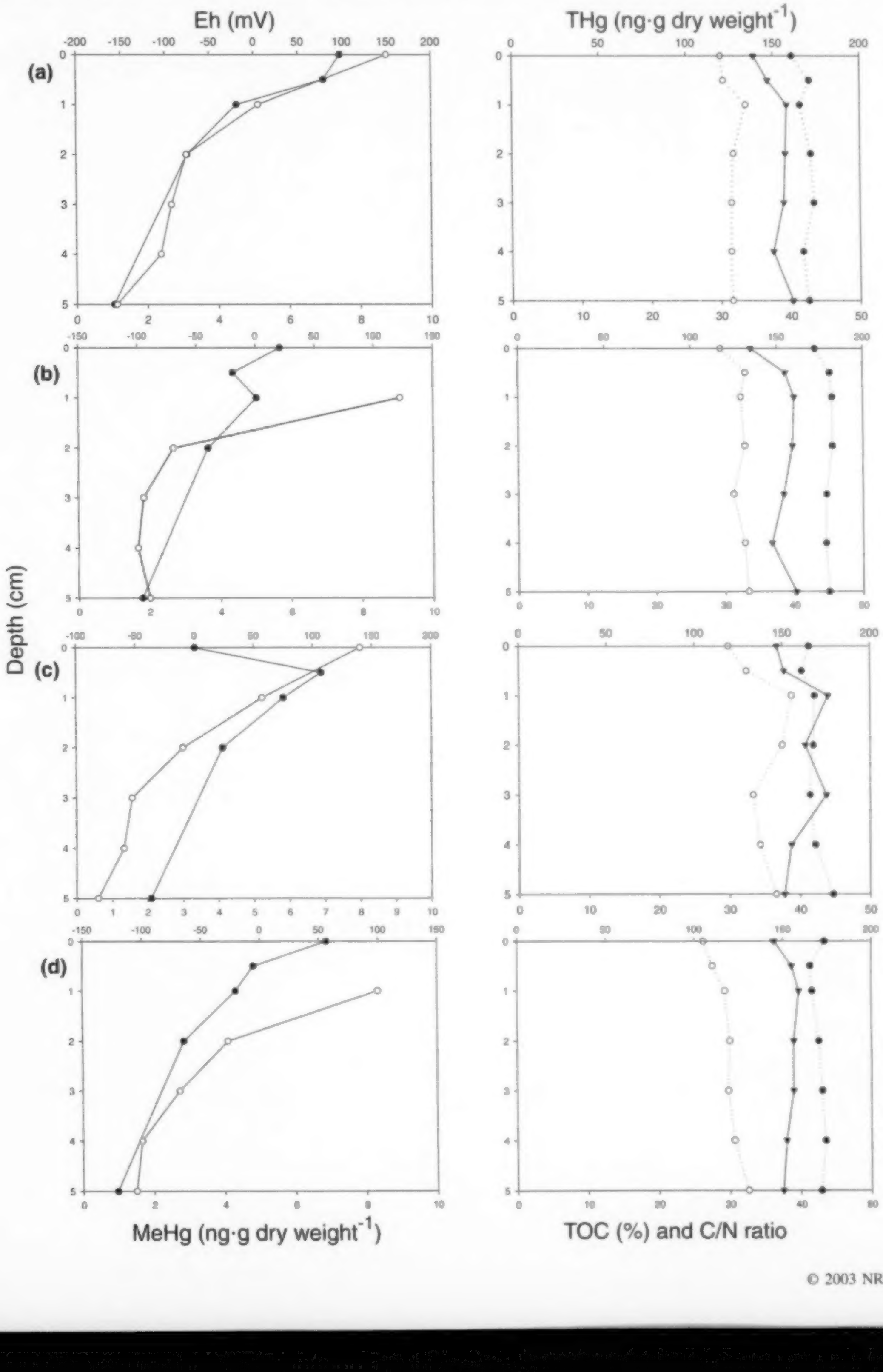


Fig. 3. Profiles of redox potentials (Eh; open circles with solid line), MeHg (solid circles with solid line) and total Hg (THg; solid triangles with solid line) concentrations, total organic carbon concentrations (TOC (%); solid circles with broken line) and atomic carbon–nitrogen ratios (C/N; open circles with broken line) in the four offshore sediment cores: (*a*) OS-1; (*b*) OS-2; (*c*) OS-3; and (*d*) OS-4.

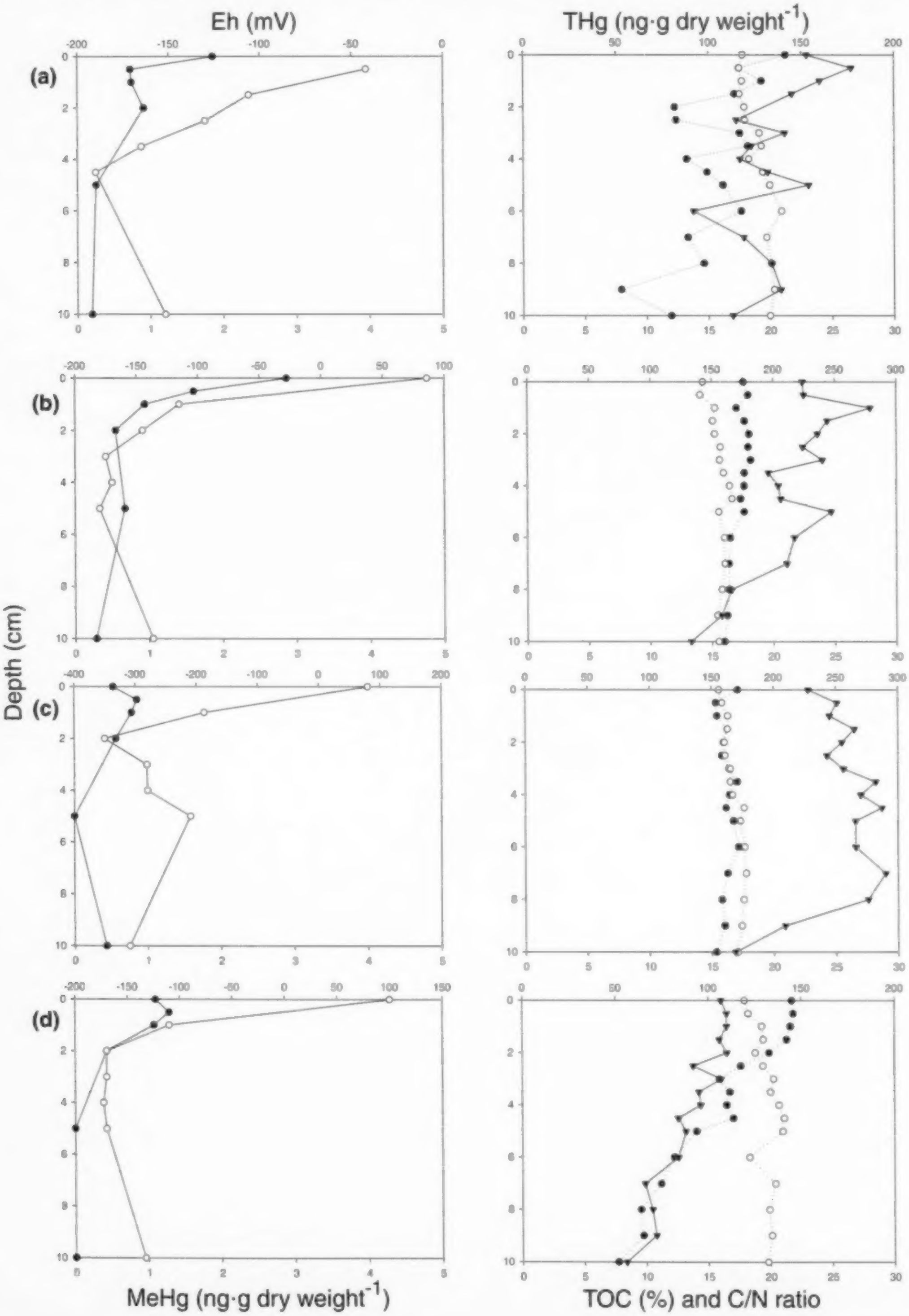


Table 1. Mean concentrations (± standard deviation) of MeHg and THg (ng·g dry weight^{-1}), fatty acid methyl esters (FAME), bacterial fatty acids (BFA), and polyunsaturated fatty acids (PUFA; the latter three are in µg·g dry weight^{-1}) at the sediment–water interface of offshore and littoral sediment sites.

	MeHg	THg	FAME	BFA	PUFA
Offshore	1.6 (±0.77)	178 (±58)	4 093 (±1721)	407 (±137)	483 (±157)
Littoral	5.8 (±1.3)	141 (±6)	13 623 (±3360)	912 (±167)	1433 (±298)

Table 2. Differences of concentrations (expressed in %, ± standard deviation) in sedimentary MeHg, fatty acid methyl esters (FAME), bacterial fatty acids (BFA), and polyunsaturated fatty acids (PUFA) between the sediment–water interface and 5-cm depth at offshore and littoral sediment sites.

Core sites	MeHg	FAME	BFA	PUFA
Offshore	90 (±9)	43 (±19)	43 (±18)	41 (±25)
Littoral	69 (±16)	27 (±13)	33 (±11)	36 (±12)

Fig. 4. Relative amount (%) of methylated Hg in the offshore (open symbols) and littoral (solid symbols) sediment cores. Data are mean values with standard deviation bars.

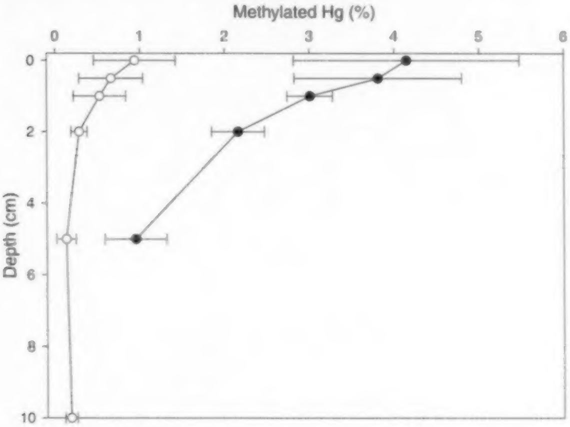
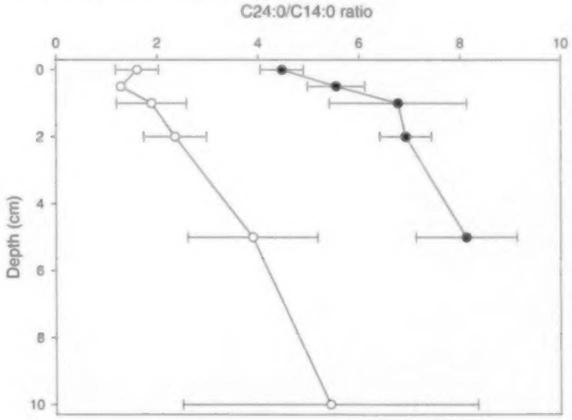


Table 3. Correlation table (using analysis of covariance to correct for sediment station) with algal biomarkers (polyunsaturated fatty acids, PUFA), total identified bacterial biomarkers (BFA), and bacterial biomarkers of Hg methylating bacteria (*iso*-15:0 and *iso*-17:0) as covariates (mg·g dry weight^{-1}) and MeHg concentrations ([MeHg]; ng·g dry weight^{-1}) and relative amount (%) of methylated inorganic Hg as dependent variables.

	Littoral sediments		Offshore sediments	
	R^2	P	R^2	P
[MeHg]				
PUFA	0.26	0.03	0.19	0.05
BFA	0.28	0.03	0.37	0.003
iso-15:0	0.14	0.13	0.34	0.005
iso-17:0	0.18	0.10	0.36	0.02
% MeHg				
PUFA	0.26	0.04	0.20	0.05
BFA	0.27	0.30	0.37	0.003
iso-15:0	0.14	0.13	0.34	0.005
iso-17:0	0.19	0.08	0.26	0.02

Note: Regressions were based on sediment samples from littoral (0, 0.5, 1, 2, and 5 cm) and offshore (0, 0.5, 1, 2, 5, and 10 cm) cores.

Fig. 5. Ratios of allochthonous (C24:0) versus autochthonous (C14:0) organic matter indicators in the offshore (open symbols) and littoral (solid symbols) sediment profiles. Data are mean values with standard deviation bars.



were significantly correlated with [MeHg] and the relative amount of methylated inorganic Hg (InHg; Table 3). At littoral sediment sites, only [PUFA] were significantly correlated with [MeHg] and the relative amount of methylated InHg. Depth of sediment segments correlated significantly with [PUFA], [bacterial FA], [*iso*-15:0], and [*iso*-17:0], and depth has not been included as a covariate to avoid problems of colinearity. The R^2 values represent the amount of variance explained by [PUFA], [bacterial FA], [*iso*-15:0], and [*iso*-17:0] after having corrected for the effect of sediment station.

Discussion

MeHg in littoral and offshore sediments

[MeHg] are higher in littoral than in offshore sediments, which is in line with findings of previous work (Ramlal et al. 1993). MeHg profiles do not follow those of InHg. We observed variable [THg] profiles at OS-1, -2, and -3, which indicates that [MeHg] are independent of the quantity of InHg, as reported in an earlier study (Kainz and Lucotte 2002). The relative amount of methylated Hg is significantly different between littoral and offshore sediments, indicating that MeHg dynamics at littoral sites vary from those at offshore sites. For littoral sediments, it is possible that deposition of terrestrially derived OM containing MeHg may have contributed to the high [MeHg]. However, although stable [TOC], [THg], and lignoceric acid concentrations in littoral sediment profiles suggest constant terrestrial OM input, [MeHg] generally decrease in all littoral cores, indicating that the quantity of terrestrially derived OM cannot predict [MeHg] in littoral sediments. Moreover, OM from macrophytic plants is unlikely to constitute an additional MeHg source to littoral sediment sites because it has been found that MeHg in rooted macrophytes is mainly taken up from sediments (Ribeyre and Boudou 1994).

Composition of OM in sediments — implications for MeHg

[MeHg] correlates significantly with [TOC] at the SWI among the various cores ($R^2 = 0.72$; $P < 0.05$) as in other studies (e.g., Regnell and Ewald 1997). However, below the SWI, correlations between decreasing [MeHg] and [TOC] were not significant ($P > 0.1$), suggesting that TOC is insufficient to predict [MeHg] in sediment cores.

Jackson (1988) measured higher [MeHg] in flooded forest sediments than in offshore sediments and attributed this difference to more labile OM in the flooded system. However, OM derived from vascular plants is known to contain recalcitrant biogenic components that can impede bacterial growth efficiencies (Benner et al. 1988). The quality of OM can be geochemically characterized by the C/N ratio. Terrestrial plant material generally contains higher C/N ratios than aquatic plants or algae (Meyers and Ishiwatari 1993). In Lake Lusignan, higher C/N ratios in littoral versus offshore sediments indicate higher contributions of terrigenous vascular plant debris. Thus, based on the high littoral C/N ratios, elevated littoral [MeHg] would appear to contradict Jackson's idea that labile OM favours the presence of higher [MeHg]. To solve this paradox, we analysed FA biomarkers to examine the source composition of OM in sediments.

Allochthonous and autochthonous fatty acid biomarkers

The C24:0/C14:0 ratios are all >1, indicating the preponderance of terrigenous OM. The ratios for the littoral sediments are at least twice as high as those offshore. A similar trend is observed for C/N ratios. In contrast, the downcore development of these two indicators is different. Although C/N ratios remain stable throughout the core profiles, C24:0/C14:0 ratios increase with each segment below the SWI, suggesting a decrease of autochthonously derived OM with respect to allochthonously derived OM. It can be stated that OM becomes more recalcitrant with depth in both offshore and littoral sediment sites.

Polyunsaturated fatty acids

Because Hg methylation is thought to be stimulated by decomposition of labile organic material (Bodaly et al. 1984; Lucotte et al. 1999), we examine the presence of highly reactive OM compounds in the sedimentary records. PUFA (e.g., ω-3 and ω-6 series) are the most important FA biomarkers of algal biomass (Desvilettes et al. 1997) and are prone to rapid degradation because of their lability (Meyers et al. 1984). Short chain FA ($\leq C_{18}$) such as labile phytoplankton biomarkers that survive degradation in the water column are preferred compounds for bacterial attack within sediments (Kawamura et al. 1987).

Higher [PUFA] in littoral sediments may be attributable to the abundance of periphytic and benthic algae. The quantity of labile algal OM biomarkers accounts for 26% and up to 20% of [MeHg] and the relative amount of methylated InHg in littoral and offshore sediments, respectively. However, although algal derived OM may provide energy-yielding substrates for Hg methylating and MeHg degrading bacteria, it does not produce or degrade MeHg in sediments.

Bacterial fatty acids

It has been found that lactate (Pak and Bartha 1998*b*) and pyruvate (Compeau and Bartha 1985) stimulate the methylation of InHg by the sulfate-reducing bacterium (SRB) *Desulfovibrio desulfuricans* (Choi et al. 1994). Analyses on total sedimentary biomass, including algal and bacterial components, are crucial because SRB cannot degrade biopolymers (Hansen 1993) and hence depend on the activities of other organisms to provide them with fermentation and degradation products. Although the decrease of [MeHg] and the relative amount of methylated InHg (between 0 and 5 cm) is less in littoral than in offshore sediments, these declines are much smaller in magnitude than the decrease of [PUFA] at both littoral and offshore sites. This contrast challenges the assumption that [MeHg] in sediments is controlled by bacterial degradation of labile OM (Lucotte et al. 1999).

Bacterial markers have been measured to be more than twice as high in littoral than in offshore sediments, and differences in [MeHg] between the two sites are even higher (3.6 times). [MeHg] and the relative amounts of methylated InHg are significantly correlated with total bacterial biomarkers. However, not all bacteria are involved in the formation of MeHg (Pak and Bartha 1998*a*); thus, we have examined the association between MeHg and FA biomarkers of the Hg-methylating bacterium *D. desulfuricans*, i.e., *iso*-15:0 and *iso*-17:0 (e.g., Taylor and Parkes 1983). In offshore sediments, [*iso*-15:0] and [*iso*-17:0] are significantly correlated with [MeHg] and the relative amount of methylated InHg. However, as observed with total bacterial biomarkers, *iso*-15:0 and *iso*-17:0 biomarkers cannot significantly predict [MeHg] in littoral sediments. Given the same concentrations of *D. desulfuricans* related biomarkers, the amount of methylated InHg varies between 1% and 5% at littoral sites, whereas it is generally less than 1% in offshore sediments. These results suggest that bacteria-mediated MeHg dynamics are higher in littoral than in offshore sediments, which may also be related to higher littoral sediment temperatures as found by Ramlal et al. (1993).

Indicators for MeHg dynamics in sediment layers

Pak and Bartha (1998*a*) found that Hg in sediments can be methylated and also demethylated by *D. desulfuricans*. Consequently, quantification of these sulfidogenic bacterial biomarkers does not relate to specific bacteria-mediated MeHg dynamics in sediments. In addition, methanogens are also known to degrade MeHg in sediments (Oremland et al. 1991). Rising gas bubbles to the water–air interface at littoral sites were indicative of methanogenic activity in sediments; however, membrane lipids of methanogens are principally isopranyl ethers of glycerol (Balch et al. 1979) and their presence could therefore not be identified by FAME signatures.

Below the SWI, decreasing [MeHg] follow increasing anaerobic conditions in sediments. The millivoltage (Eh, mV) drop is highest within the first 2 cm below the SWI, and the most elevated [MeHg] are generally found in these strongly oxygen reducing segments. This observation is in agreement with other studies in which maximum methylation rates have been measured at oxidative anaerobic sediment interfaces (e.g., Watras et al. 1995). The decrease of [MeHg] in the anaerobic sediment layers may be related to the activity of bacterial populations involved in demethylation of MeHg (Oremland et al. 1991; Pak and Bartha 1998*a*). However, the decrease of bacterial biomarkers and [PUFA] in sediment layers is smaller than that of [MeHg], indicating that labile OM is not quantitatively associated with bacterial MeHg dynamics in anaerobic zones.

In addition, myristic and palmitic (C16:0) acids exist in phytoplankton, zooplankton, and fecal pellets (Volkman et al. 1989) and contribute up to 16% and 20% of the FAME in littoral and offshore sediments, respectively (Kainz 2001). The relative contribution of those lake biota signatures is thus similar at both littoral and offshore sediments. Because of the shallow water depth at littoral sites, it appears unlikely that the sedimentation of waterborne MeHg is more than three times higher at the littoral than at the offshore SWI. In fact, [MeHg] in zooplankton organisms from the littoral site are lower than those from offshore sites (Kainz et al. 2002), suggesting that high [MeHg] in the littoral sediments are predominantly related to in situ processes. In contrast, biotic processes such as removal of MeHg-rich offshore zooplankton by predators may account for low [MeHg] at the SWI of offshore sites. Finally, although diffusion of dissolved MeHg from sediments to the water column cannot rule out higher [MeHg] at the top sediment layers, it is clear that the distribution of MeHg in sediment layers cannot be explained by the composition of OM.

In conclusion, the use of lipid biomarkers to identify OM sources in sediment records of Lake Lusignan is more detailed and therefore more informative than the binary C/N indicator. As a result, we could demonstrate that (*i*) the amounts of algal and bacterial OM are significantly higher at littoral than at offshore sites and (*ii*) the amount of recalcitrant terrestrial OM is unrelated to [MeHg] in sediment profiles. Although [MeHg], the amount of labile OM, and the quantity of sulfidogenic bacterial biomarkers were higher at littoral sites, FAME biomarkers could not identify the presence of Hg-demethylating methanogenic bacteria. This study illustrates that microbial dynamics involved in producing and degrading MeHg in lacustrine sediments are complex and cannot be predicted solely by the quantification of FAME biomarkers in *D. desulfuricans* or by FAME biomarkers in the OM itself.

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